The American Midland Naturalist

Devoted to Natural History

Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

Editor

Theodor Just, Botany

Associate Editors

Carroll Lane Fenton, West Liberty, Iowa ---------- Paleontology

John Hobart Hoskins, Cincinnati, Ohio ---------- Botany

Remington Kellogg, Washington, D. C. ---------- Paleontology and Zoology

Marcus Ward Lyon, Jr., South Bend, Ind. ---------- Zoology

Francis Joseph Wenninger, C.S.C. ---------- Zoology

Vol. 18, 1937

UNIVERSITY OF NOTRE DAME

Notre Dame, Indiana

CONTENTS

No. 1, JANUARY, 1937

Studies on the Muscles of the Pelvic Appendage in Birds—*George Elford Hudson* 1

Aulopora: a Form-Genus of Tabulate Corals and Bryozoans—*Mildred Adams Fenton* and *Carroll Lane Fenton* ---- 109

Species of Aulopora from the Traverse and Hamilton Groups—*Mildred Adams Fenton* ---- 115

Aulocaulis, a New Genus of Auloporoid Corals—*Mildred Adams Fenton* and *Carroll Lane Fenton* ---- 119

Mid-Tertiary Vertebrates from the Texas Coastal Plain: Fact and Fable—*Horace Elmer Wood, 2nd* and *Albert Elmer Wood* ---- 129

Tracks from the Pliocene of West Texas—*C. Stuart Johnston* ---- 147

A Skull of Teleoceras fossiger Cope, from the Clarendon Beds of Donley County, Texas—*C. Stuart Johnston* ---- 152

Spores from the Pennington Coal, Rhea County, Tennesssee—*Willard Berry* ---- 155

No. 2, MARCH, 1937

Ecological Studies on Selected Marine Intertidal Communities of Monterey Bay, California—*Willis G. Hewatt* ---- 161

Further Studies on North American Gyrodactyloidea—*Justus F. Mueller* ---- 207

Two New Blind Isopods from Northeastern Oklahoma—*H. D. Chase* and *A. P. Blair* ---- 220

The Genera Cyperana and Paluda (Homoptera-Cicadellidae)—*Dwight M. DeLong* ---- 225

New Moss-Mites, Chiefly Midwestern—II.—*Arthur Paul Jacot* ---- 237

The Biology of Physa anatina Lea, a Snail Living in a Sewage Treatment Plant —*Thelma Fish Brown* ---- 251

A Season with Holbrook's Frog (Pseudacris ornata)—*Francis Harper* ---- 260

Observatioins on Bufo cognatus with Special Reference to the Breeding Habits and Eggs—*Arthur N. Bragg* ---- 273

Ecological Observations on Amphibians and Reptiles Collected in Southeastern Oklahoma during the Summer of 1934—*Albert H. Trowbridge* ---- 285

Mustela cicognanii, the Short Tailed Weasel, Incorrectly Ascribed to Ohio—*E. Raymond Hall* ---- 304

Book Reviews ---- 305

No. 3, MAY, 1937

Benjamin Franklin Bush—*Ernest J. Palmer* ---- i-vi

Morphology and Cytology of Vallisneria spiralis L.—*Samuel Wenger Witmer* ---- 309

Andropogonetum Hempsteadi: a Long Island Grassland Vegetation Type—*Stanley A. Cain, Mary Nelson,* and *Walter McLean* ---- 334

Cantillas Canyon of Lower California: Its Geography and Botanical History—*Joseph Ewan* ---- 351

A Remarkable Colony of Coastal Plain Plants on the Cumberland Plateau in Laurel County, Kentucky—*E. Lucy Braun* ---- 363

Soil Preferences of Some Upland Deciduous Trees in Central Minnesota—*R. F. Daubenmire* ---- 367

Herpetological Notes from Central Kansas—*Chapman Grant* ---- 370

The Birds of Dakota County, Nebraska—*T. C. Stephens* ---- 373

Cardiac Inversion and Translocation in a New-born Calf—*Charles D. Howell* and *F. Gardner Lynn* ---- 398

The Effect of the Winter of 1935-36 on Wisconsin Quail—*Aldo Leopold* ---- 408

Winter Feeding at Faville Grove, 1935-36—*Arthur S. Hawkins* ---- 417

Post Hurricane Sea Shore Observations—*E. M. Kindle* ---- 426

Cambrian Calcareous Algae from Pennsylvania—*Carroll Lane Fenton* and *Mildred Adams Fenton* ---- 435

Some Devonian Auloporoids from the Ohio Valley—*Vladimir J. Okulitch* ---- 442

Trilobite "Nests" and Feeding Burrows—*Carroll Lane Fenton* and *Mildred Adams Fenton* ---- 446

Olivellites, a Pennsylvanian Snail Burrow—*Carroll Lane Fenton* and *Mildred Adams Fenton* ---- 452

Archaeonassa: Cambrian Snail Trails and Burrows—*Carroll Lane Fenton* and *Mildred Adams Fenton* ---- 454

Pleistocene Fossils from Newfoundland Collected by Expeditions from Princeton University—*Horace G. Richards* ---- 457

Additional Fauna of Edson Quarry of the Middle Pliocene of Kansas—*Claude W. Hibbard* ---- 460

The Skull of Mylodon Harlani from the Lower Pleistocene of West Texas—*C. Stuart Johnston* ---- 465

Book Reviews ---- 470

No. 4, JULY, 1937

Stratigraphy and Structure of the Area of Disturbed Ordovician Rocks near Kentland, Indiana—*Robert R. Shrock* ---- 471

Paleontology of the Disturbed Ordovician Rocks near Kentland, Indiana—*Robert R. Shrock* and *Gilbert O. Raasch* ---- 532

Skull of Musk-Ox, Genus Symbos, from Montgomery County, Indiana—*Marcus Ward Lyon, Jr.,* and *Fred T. Hall* ---- 608

Ectoparasites of the Blunt-Nosed Minnow (Hyborhynchus notatus)—*John D. Mizelle* ---- 612

The Genus Craminella (Homoptera-Cicadellidae)—*Dwight M. DeLong* and *Carl O. Mohr* ---- 622

Evolutionary Trends, Ecological Notes, and Terminology of the Large-Winged Mites of North America—*Arthur Paul Jacot* ---- 631

Diatoms from Lake Michigan—I.—*B. V. Skvortzow* ---- 652

An Occurrence of Sphaerotheca lanestris in Mexico—*G. M. Watkins* and *C. H. Muller* ---- 659

Phytosociological Studies in the Pinelands of Southeastern Louisiana—*William T. Penfound* and *Allan C. Watkins* ---- 661

Three New Plants from Texas and Mexico and Some Recent Additions to the Texan Flora—*Paul C. Standley* ---- 683

Book Reviews ---- 685

No. 5, SEPTEMBER, 1937

The Life-Forms of the Flowering Plants of Indiana—*Sr. Elizabeth Seton McDonald* ---- 687

The Lemnaceae of Indiana—*Lawrence E. Hicks* ---- 774

Studies in Penstemon V. The Section Peltanthera—*David D. Keck* ---- 790

The Orchidaceae of the Rocky Mountains—*Louis O. Williams* ---- 830

Studies in Mexican and Central American Plants—*Cornelius H. Muller* ---- 842

The Spider Genus Lepthyphantes in the United States—*Helen M. Zorsch* ---- 856

New Echinoderms from the Devonian Cedar Valley Formation of Iowa—*Merrill A. Stainbrook* ---- 899

Description of a New Horse, Calippus regulus from the Clarendon Beds of Donley County, Texas—*C. Stuart Johnston* ---- 905

Book Reviews ---- 908

No. 6, NOVEMBER, 1937

The Filamentous Algae of the West End of Lake Erie—*Lewis Hanford Tiffany* ---- 911

The Plants of Mount Rainier National Park, Washington—*Harold St. John* and *Fred A. Warren* ---- 952

Plants as Indicators of Climate in Northeast Mexico—*Cornelius H. Muller* ---- 986

Vegetative Reproduction in Conifers—*J. E. Potzger* ---- 1001

Some Blood Parasites from Nebraska Birds—*G. Robert Coatney* and *Robert L. Roudabush* ---- 1005

Notes on the Natural History of Several Marine Crustacea—*G. E. MacGinitie* ---- 1031

Observations on the River Shrimp, Macrobrachium ohionis (Smith)—*Gordon Gunter* ---------- 1038

The Life-history and Habits of the Digger-wasp Ammobia ichneumonea (Linn.)—*John A. Frisch, S.J.* ---------- 1043

Natural History of the Ambystomid Salamanders of Illinois—*D. John O'Donnell* 1063

Some Habits of Southern Fur-Bearers as Indicated by Trapping—*Lee E. Yeager* ---------- 1072

Burrows and Trails from Pennsylvanian Rocks of Texas—*Carroll Lane Fenton* and *Mildred Adams Fenton* ---------- 1079

Species and Geographic Distribution of the Lichadacea—*Fred B. Phleger, Jr.* --- 1085

A Method of Generic Comparison—*Fred B. Phleger, Jr.* ---------- 1093

Secondary Blinding Among the Phacopid Trilobites and its Significance—*David M. Delo* ---------- 1096

Book Reviews ---------- 1103

Dates of Publication

Volume 18, 1937

Number 1 January	January 7
Number 2 March	February 23
Number 3 May	April 30
Number 4 July	July 28
Number 5 September	September 18
Number 6 November	November 10

The American Midland Naturalist

Devoted to Natural History, Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

Contents

Studies on the Muscles of the Pelvic Appendage in Birds—*George Elford Hudson*.. 1

Aulopora: a Form-Genus of Tabulate Corals and Bryozoans—*Mildred Adams Fenton* and *Carroll Lane Fenton* 109

Species of Aulopora from the Traverse and Hamilton Groups—*Mildred Adams Fenton* 115

Aulocaulis, a New Genus of Auloporoid Corals—*Mildred Adams Fenton* and *Carroll Lane Fenton* 119

Mid-Tertiary Vertebrates from the Texas Coastal Plain: Fact and Fable—*Horace Elmer Wood, 2nd,* and *Albert Elmer Wood* 129

Tracks from the Pliocene of West Texas—*C. Stuart Johnston* 147

A Skull of Teleoceras fossiger Cope, from the Clarendon Beds of Donley County, Texas—*C. Stuart Johnston* 152

Spores from the Pennington Coal, Rhea County, Tennessee—*Willard Berry* 155

Vol. 18 JANUARY, 1937 No. 1

EDITORIAL STAFF

THEODOR JUST,.....*Botany (Ecology, Taxonomy)*
Editor, University of Notre Dame

CARROLL LANE FENTON,.....*Invertebrate Paleontology*
West Liberty, Iowa

JOHN HOBART HOSKINS,.....*Botany (Morphology, Paleobotany)*
University of Cincinnati, Cincinnati, Ohio

REMINGTON KELLOGG,.....*Vertebrate Paleontology and Zoology*
U. S. National Museum, Washington, D. C.

MARCUS WARD LYON, JR.,.....*Mammalogy*
South Bend, Indiana

FRANCIS JOSEPH WENNINGER, C.S.C.,.....*Invertebrate Zoology*
University of Notre Dame

NOTE:—THE AMERICAN MIDLAND NATURALIST, published from the biological laboratories of the University of Notre Dame, is primarily, though not exclusively devoted to the Natural History of the Middle West. A wide selection of papers on botany, paleontology and zoology is published in bi-monthly issues, six of which make up a volume.

Fifty reprints will be furnished free of charge to contributors. Additional reprints should be ordered when proof is returned and may be had at cost price.

The following numbers are out of print: vol. 2, (1, 2, 8, 10); vol. 3, (1-3, 7-9); vol. 4, (1-7); vol. 6, index, title page; vol. 9, (9); vol. 10, index, title page; vol. 11, (1). All others available, 30 cents per copy. Complete volumes: $3.00; volumes 7, 13, and 14, $1.50 each; vol. 15 $2.00, single issues 35 cents; vol. 16 $3.00, single issues 50 cents; vol. 17 $4.50, part 1 $2.00, nos. 2-6 50 cents each; vol. 18 $3.00, single issues 50 cents.

Exchanges for journals, special volumes or duplicate books, and specimens, should be arranged directly through the editorial office at the University of Notre Dame, where subscriptions also are received. Offers should accompany request for exchange.

For citation use this abbreviation: *Amer. Midl. Nat.*

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103, Act of October 3, 1917, authorized on July 3, 1918.

Benjamin Franklin Bush

1858-1937

Benjamin Franklin Bush†

Ernest J. Palmer

The death of Benjamin Franklin Bush at Independence, Missouri, February 14, 1937, marked the end of a long and in many ways a remarkable career in the field of botany.

Born in Columbus, Indiana, Dec. 21, 1858, the future botanist moved to Independence with his mother, Mrs. Henrietta Bush, in 1865; and Jackson County, of which Independence is the county seat, continued to be his home up to the time of his death. His life-long study of the plants of Jackson County resulted in it becoming one of the best known sections of the United States from the botanical standpoint, and his writings and plant collections made the name of the insignificant village of Courtney, where he long resided, familiar to botanists almost throughout the world.

Western Missouri was a frontier country at the close of the Civil War, and nowhere had gorilla warfare been carried on more fiercely than in that section. Kansas City was still a struggling new town, although the older settlement of Independence had been a trading point of importance for many years, and it was the outfitting and starting place for most of the western explorers, traders, and trappers. The Missouri Pacific railway had just been built from St. Louis, and it is said that Bush and his mother came on the first train that ran over the line. A short time after going to Missouri, Mrs. Bush was married to Robert B. Tindall, a pioneer florist who built and operated the first greenhouse in Independence. And young Bush's early interest in plants was no doubt due in some measure to his experience there as assistant to his step-father.

Bush was a born naturalist, and in the country about Independence he found a most interesting field for exploration and study. Within a radius of a few miles were areas of open prairie, upland woods, rocky glades, and numerous creeks running down to the Missouri River which formed the northern boundary of the county. The wild life was rich and varied both in plants and animals, due largely to the proximity of the great river. Many unusual species of trees and smaller plants grew along the high limestone bluffs or in the rich woods below them; springs issuing at places spread out into small bogs or flowed into lakes and sloughs formed by old channels or ox-bow bends of the river; while an almost impenetrable growth of trees, shrubs, vines, and herbaceous plants covered large areas of the flood plains. All of these conditions contributed toward supporting a rich flora, and they also furnished protection and an abundant food supply for many small mammals, birds, and reptiles, and the lower forms of land and aquatic life. Beautifully preserved fossils could be found in many of the beds of limestone and sandstone of the Pennsylvanian series exposed in bluffs and quarries; and evidences of the former Indian inhabitants were abundant in the form of flint arrow-heads and other implements found in the fields or in graves and small mounds.

Here was indeed a happy hunting ground for a young naturalist, and Bush became interested in all these things. One of his earliest interests was in the birds, and he came to know all of the resident and migrant species of the region not only by sight but also by their calls and songs. The collection of birds' eggs that he made at this time became valuable in later years, since it contained sets of many species no longer to be found in the region. Like other naturalists of the time, he was impressed by the enormous flights of passenger pigeons that cast shadows like passing clouds; and he also recalled the great abundance of prairie hens, and the Carolina paroquets that sat on stumps in the recent clearing, and were so tame or so stupid that it was possible to approach and catch them under a coat or hat. Bush's interest in birds continued through life, although it was later subordinated to his study of plants.

This must also have developed at an early age, since his first catalogue of the plants of Jackson County was published in 1882.

A copy of Wood's Class-book of Botany fell into his hands, and with the aid of this he tried to identify the native plants. Only a small proportion of them were mentioned, however, in this work, and indeed no flora of the time was at all adequate. In his eagerness to learn more about the plants of the county, Bush became a correspondent of Dr. George Engelmann and Dr. Asa Gray; and in later years his correspondents included many of the leading botanists of America and a number abroad. In 1886, when Professor S. M. Tracy, of the State University of Missouri, published the first catalogue of the plants of the state, Bush's lists and notes were the chief source of information for the plants of Jackson and adjoining counties. Reverend Cameron Mann, while a resident of Kansas City, was also an enthusiastic student of the local flora, and Bush accompanied him on many botanical excursions. In 1885 they collaborated in publishing a supplement to the Flora of Jackson County. A few years later he formed a botanical friendship with Kenneth K. Mackenzie, a keen student of botany who had begun an independent study of the flora about Kansas City. Together they botanized in all parts of the county throughout several seasons collecting material for the Manual of the Flora of Jackson County, which Mackenzie brought out in 1902, with Bush as associate author. Mackenzie and Bush also made several botanical trips together in different parts of Missouri, and they published jointly several papers on the plants of the state.

In 1891 and 1892 Mr. Bush was employed to assist in collecting specimens of woods and other material for the Missouri forestry exhibit at the Columbian Exposition, Chicago, and this work took him into different parts of the state and also brought him into contact with a number of other botanists. While staying in St. Louis he made the acquaintance of Henry Eggert, an experienced collector and a discriminating botanist, and Bush acknowledged his indebtedness to him for much information about plants and methods of collecting and preserving them. Later, as a collector for the Missouri Botanical Garden, he visited many remote parts of the state and made extensive collections also in the counties of Clark, Atchison, McDonald, and Dunklin, occupying the four extreme corners. As a result of these explorations scores of species not previously known in the state were added to the flora, and a number were discovered that proved new to science. In 1899 and for about ten years thereafter he made collecting trips each season for the Arnold Arboretum, gathering notes and material on trees and shrubs, with particular attention to the genus *Crataegus;* and his work was recognized by Professor Charles S. Sargent as a valuable aid to him in his studies of this and other genera. Besides covering much of the state of Missouri, he travelled and collected extensively in Arkansas, Oklahoma, Texas, and several other states. Bush also made general collections of plants on all of these trips for distribution to other herbaria.

Although botany remained his chief interest throughout life, the demands of a growing family made it necessary for him to engage in some business more profitable than that of a plant collector; and early in the eighteen-nineties he established a general store and was appointed postmaster at Courtney. This continued to be his home for more than forty years; and it was here, in the little time that he could take from his duties as merchant and postmaster, that most of his botanical writing was done and many of his sets of plants were prepared and sent out.

Courtney had many advantages for the study of local botany: located 16 miles east of Kansas City, on the main line of the Santa Fe railroad, and four miles north of Independence, it lies in a great bend of the Missouri River, with the bluffs on one side and the river on the other, both within easy walking distance. Besides the rich native flora, new plant immigrants were constantly appearing about the great railway center of Kansas City or on the gravel bars or in the flood plains of the river. So when trips further afield were denied him, Bush was able to find things of interest almost in his back yard, and seldom in the season was his plant press empty. Here many well known and famous botanists, as well as local naturalists and sometimes reporters from the city, came to visit and to interview him; and not a few of them remained to accept his hospitality and to go out on collecting trips with him.

The amount of botanical work that he was able to accomplish under the circumstances, and without the aid of a large botanical library or herbarium, was a source

of astonishment to many of his visitors. Entering the store, he might be found working on a collection of plants or on a botanical paper, with half a dozen books, plant labels, material, and manuscript spread out on the counter. This work had to be laid aside at intervals on the arrival of the mail, to be sorted and distributed to waiting patrons, or it might at any time be interrupted by a customer coming in to buy a pair of shoes or overalls, a plug of tobacco, or a bill of groceries; and the bundle of plants or manuscript would then be hurriedly thrust on a shelf or under the counter, to be brought out and the work resumed at the first opportunity.

The writer first became acquainted with Mr. Bush in 1900, and we met the following year. At that time I was a student at the Webb City (Missouri) Baptist College, with an early bent for natural history and a particular interest in geology. A copy of a paper by Bush, on the Trees, Shrubs, and Vines of Missouri, happened to fall into my hands, and this stimulated an interest in the local species. In the introduction the author requested that teachers, horticulturists, or anyone interested in the woody plants of the state, send specimens to him for identification, for the purpose of bringing about a better knowledge of the flora of the state and of the distribution of the trees and shrubs. Finding many plants unknown to me, I decided to take advantage of the opportunity, and mailed a small package of twigs and leaves to him at Independence. Several weeks passed and I had almost given up hope of a reply, when one day a letter came from Columbia, Texas, where my letter had been forwarded to Mr. Bush, who was then on a collecting trip for the Arnold Arboretum. In due time I received identifications of the specimens and was invited to send others, which I did from time to time throughout the year. About that time Professor Sargent was becoming very much interested in the North American species of *Crataegus*, and Bush asked me to look out for the various sorts to be found about Webb City.

The following spring I was thrilled by receiving a letter from Mr. Bush saying that he was starting south on another collecting trip that would take him through southwestern Missouri, and that he would like to stop and see me, if convenient. He arrived early in April with field press and a complete collecting outfit. The hawthorns and many other trees were just coming into bloom and young leaf, and the locality proved to be so interesting that Bush remained as a guest at my father's home for nearly a week, diligently collecting in all directions about the place. Whenever possible I accompanied him on his excursions, and as his eager assistant, guide and pupil, I soon became deeply interested in the flora. Upon leaving for the South, Mr. Bush left me a supply of dryers, and having rigged up a crude field press, I was irrevocably launched as a local collector. This was the first of a number of visits Bush paid to Webb City, and at various times I accompanied him on more extended collecting trips to other parts of Missouri. His visits were always looked forward to with the greatest pleasure, and as I came to know him better, my admiration grew for his wonderful knowledge of plants in the field and for his energy and patience in adding to his store of knowledge.

Mr. Bush was an ideal companion on field excursions. His indefatigable energy, quiet enthusiasm, and keenness of observation were a stimulus and an inspiration; his patience and good nature were never ruffled by the most trying circumstances; and his store of anecdotes, based largely upon his own experiences and observations or upon the work and personalities of other naturalists whom he had met, furnished unfailing interest. I was particularly impressed with the fact that no matter what the subject of conversation or with what eagerness it was being pursued, never for a moment did it seem to interfere with his alertness and faculties of observation. At one moment he would pause to listen to the call of a distant bird or to watch the movements of something stirring in the grass or trees; at another he would be pointing out the effects of weather or the work of insects in the forest; and in his general survey of the trees above and the smaller plants beneath, he seemed to miss no detail and would constantly be discovering something of interest or significance and pausing to investigate it. Indeed this very keenness of observation and ability to see the minutest distinctions and departure from the typical forms in plants may have at times been a weakness when he undertook to write descriptive papers, as he was likely to see and regard as specific differences slight variations that a more conservative investigator would have overlooked.

As much of his botanical collecting was done before the days of automobiles and good roads, or in sections of the country to which they had not penetrated, most of his long distance traveling was by train or stage. Having established a base in some favorable locality where he might remain for several days or weeks, he would explore the surrounding country in all directions, often walking and climbing for many miles through the wildest and most difficult places. On his field trips he always carried a wooden press secured by straps and filled with a large supply of papers and dryers. When this was well filled with plants at the end of a long day, it became a sizable load; and after the fatigues of the day he would often work far into the night arranging his notes and collections.

His faculty for finding out and exploring some of the most remote and inaccessible localities where rare plants grew and where no botanist had ever before penetrated amounted to an instinct, and this was one of the secrets of his success. Some of his favorite collecting places were near Swan, Eagle Rock, Monteer Campbell, and Noel, Missouri, Sapulpa, Indian Territory, Moark, Varner, and Fulton, Arkansas, and Larissa and Columbia, Texas. The building of modern highways and closer settlement of the country have wrought great transformations, and some of these places are easily accessible today, but at the time of Bush's early visits living conditions were extremely primitive, and the appearance and activities of a stranger, and especially one on so unusual a quest, occasioned not only interest but suspicion. Like most successful naturalists, Bush was extremely adaptable and ready to put up with meager accommodations, and his faculty for establishing friendly relationships with strangers was one of his greatest assets. He was an enthusiastic and successful fisherman, and whenever time and opportunity permitted he indulged in this pastime. There were times when so many plants had accumulated that it was necessary to wait until presses could be emptied; or sometimes he would go out at night with a companion or a party of local fishermen to some creek or bayou where he would prove his skill as an angler; and this always went a long way toward winning friendship and confidence. One of Bush's axioms was that to find really good fishing it was necessary to be a long way from a good hotel; and he applied the same principle to the selection of localities for plant collecting.

A good deal of imagination and exaggeration has gone into stories about moonshiners. But the illicit still was really an important industry in some sections even before the days of prohibition; and in localities where it flourished a stranger was likely to be under suspicion as a revenue officer or spy. One of the anecdotes Bush related concerned an experience of this sort in a remote section of the Ozarks where he went to collect on several occasions. Here he found lodging with the local merchant, who was also postmaster and justice of the peace. And years afterwards when they had become better acquainted, his host confided to him that at the time of his first visit, he with other enterprising citizens having a still in operation in a near-by hollow, had deputized one of their number armed with a squirrel rifle to follow the mysterious stranger about on all his wanderings and to ascertain his real business.

At his home at Courtney, where he was acquainted through long residence and his excursions afield with nearly everyone for miles around, his interest in natural history—or in "weeds, bugs, snakes, and things"—although known and respected, always remained a source of wonder and of mystery to many of his neighbors. As a small business man, farmer, and neighbor, he was better understood and well liked, and he had many friends among all classes.

The Santa Fe Railway employed a number of Mexican laborers on construction and maintenance work about Courtney, and shortly after Bush established his business there, a large cement plant was built a short distance up the river that also brought in many transient Mexican and Italian laborers. Through arrangements with the companies Bush furnished supplies to some of these workers, and others became voluntary customers. He managed to pick up enough Spanish and Italian to communicate with those who knew little or no English, and this was a great aid to him in dealing with them. As they came to know and to trust him, many of them came to him for advice in business affairs and in their minor clashes with the law, and he freely gave much of his time to looking after their interests and in acting as scribe and advisor.

In Independence and Kansas City his botanical work received much recognition, even though the nature of it was little understood. His work and fame became in time a source of local pride. Sunday editions of the city papers had illustrated stories of him and of his botanical work, and there were frequent press references to his goings and comings. He was for a number of years unofficial botanical adviser to the park system of Kansas City and had the privilege of collecting in all the public parks. His portrait was hung in the public library of his early home town of Independence. Thus, as the years passed his fame spread, not only in scientific circles, but also among his neighbors, and he became more and more an institution in the community—the Sage of Courtney, and a prophet not without honor in his own community. The value of his contributions toward a better knowledge of the flora of those parts of the country where his field of activities lay has been generally recognized in the scientific world, and scores of species which he discovered have been namd in his honor.

Among the large number of plants new to science that were first collected or recognized by Bush are the following: *Tradescantia hirsuticaulis* Bush, *Iris foliosa* Mack. & Bush, *Heuchera puberula* Mack & Bush, *Quercus arkansana* Sarg., *Chenopodium missouriense* Aellen, *Delphinium Treleasei* Bush, *Hamamelis vernalis* Sarg., *Crataegus missouriensis* Britton, *Crataegus padifolia* Sarg., *Callirhoe Bushii* Fernald, *Viola missouriensis* Greene, *Fraxinus profunda* Bush, *Scutellaria Bushii* Britton, *Aureolaria calycosa* (Mack. & Bush) Pennell, *Viburnum affine* Bush, and *Echinacea paradoxa* (Norton) Britton.

One of his most important discoveries, although not of a new species, was that of the cork wood (*Leitneria floridana* Chapm.) in the swamps of southeastern Missouri. This rare and interesting tree had previously been known only from collections made by Dr. Chapman along the Florida coast and from a doubtful specimen said to have been collected by Drummond in southeastern Texas. Bush first heard of it from fishermen who used the light wood as floats for their nets. He found it growing locally abundant in some of the deep swamps of Dunklin County, Missouri, and later extended its range into northeastern Arkansas. It has since been rediscovered along the lower Brazos River, in Texas, and at a few other widely scattered stations, but it remains one of the rarest of North American trees.

Benjamin Franklin Bush was most widely known and will probably be best remembered as a botanical collector and explorer. The many thousands of well-prepared sheets of plants collected by him which have found their way into nearly all the herbaria of the world will be a constant reminder of his work; the large number of plants previously unknown to science which he discovered, and many of which he described, as well as those described by others and bearing his name, will emain a monument to him. His work on the flora of Jackson County and of the entire state of Missouri, both through his collections and writings, was particularly outstanding and valuable, and his name will always rank high in the annals of Missouri botany.

Bush was the author of a large number of botanical papers which appeared in various scientific periodicals; these included plant lists, technical papers on a number of plant genera, and shorter critical notes. The following list of titles and references is probably incomplete but it includes his more important publications and such minor notes as have come to our attention:

Notes from Independence, Missouri. Bot. Gaz. **7**:24, 1882.

Flora of Jackson Co. 16 pp. Independence, 1882.

Missouri notes. Bot. Gaz. **9**:63, 1884.

Report on the botany of Jackson County. Mo. Hort. Soc. Rept. (1888) **31**:370-372, 1889.

Distribution of the trees, shrubs, and vines of Jackson County, Missouri. Kansas City Scientist **5**:161-164, 1891.

Notes on a list of plants collected in southeastern Missouri in 1893. Ann. Rept. Mo. Bot. Gard. **5**:139-153, 1894.

Hybrid oaks in western Missouri. Garden and Forest **8**:32-33, 1895.

A new hybrid oak in the Indian Territory. Garden and Forest **8**:463. 1895.

A list of the trees, shrubs, and vines of Missouri. Mo. Hort. Soc. Rept. (1894) **37**:353-394, 1895.
Notes on the mound flora of Atchison County, Missouri. Ann. Rept. Mo. Bot. Gard. **6**:121-134, 1895.
Quercus Phellos x rubra in Missouri. Garden and Forest **8**:379, 1895.
Notes on the botany of some southern swamps. Garden and Forest **10**:514-516, 1897.
Native and garden Delphiniums of North America, in Davis, K. C., Minn. Bot. Studies **2**:444, 1900.
A list of the ferns of Texas. Bull. Torr. Bot. Club **30**:343-358, 1903.
A new genus of grasses. Trans. Acad. Sci. St. Louis **13**:175-183, 1903.
The genus Othake Rafinesque. Ibid. **14**:171-180, 1904.
The Texas Tradescantias. Ibid. **14**:181-193, 1904.
The American species of Fuirena. Ann. Rept. Mo. Bot. Gard. **16**:87-98, 1905.
Two new Texas Tradescantias. Ibid. **16**:100-101, 1905.
Some new Texas plants. Ibid. **17**:119-125, 1906.
The Missouri Saxifrages. Ibid. **20**:138-140, 1909.
The Missouri Rhexias. Rhodora **13**:166-168, 1911.
Notes on Box Elder. Am. Midl. Nat. **3**:148-150, 1913.
A new Antennaria. Ibid. **3**:352-353, 1914.
The Missouri Argemonies. Ann'ls. Mo. Bot. Gard. **3**:309-318, 1916.
The genus Euthamia in Missouri. Am. Midl. Nat. **5**:157-177, 1918.
The Missouri Muhlenbergias. Ibid. **6**:17-26, 33-49, 57-77, 81-97, 1919.
Some species of Podosemum. Ibid. **7**:29-41, 1921.
A new Viburnum. Ibid. **9**:1-3, 1924.
The Missouri species of Elymus. Ibid. **10**:49-88, 1926.
Notes on trees and shrubs of Missouri. Ibid. **10**:133-158, 1926.
The Marsh Hawk. Ibid. **10**:297-299, 1927.
The glabrate species of Tilia. Bull. Torr. Bot. Club **54**:231-248, 1927.
Some species of Viburnum. Ibid. **10**:225-243, 1927.
A great blunder. Am. Midl. Nat. **10**:400-403, 1927.
The species of Polygonatum. Ibid. **10**:385-400, 1927.
The Missouri Artemisias. Ibid. **11**:25-39, 1928.
Notes on trees and shrubs of Missouri. Ibid. **11**:101-124, 1928.
Some species of Saxifraga. Ibid. **11**:213-235, 1928.
The Mexican species of Tilia. Ibid. **11**:343-360, 1929.
Notes on Aesculus species. Ibid. **12**:19-26, 1930.
Ferns of Oklahoma. Ibid. **12**:91-112, 1930.
Francis Daniels' Carices. Ibid. **12**:185-194, 1931.
Francis Daniels' grasses. Ibid. **12**:343-362, 1931.
Shepard's Greene County flora—An unpublished list of plants of Greene County, Missouri, by Professor Edward M. Shepard, Springfield, Missouri. Ibid. **12**:488-498, 1931.
Some Lacinaria species. Ibid. **12**:312-318, 1931.
The Sugar maples. Ibid. **12**:499-503, 1931.
Tilia, in SMALL, J. K., Man. S. E. Fl. 1933.
More about Acer saccharum Marshall. Am. Midl. Nat. **15**:784, 1934.
Professor Shepard's trees of Greene County. Ibid. **15**:581-585, 1934.
Francis Daniels' flora of Columbia, Missouri. Ibid. **16**:83-93, 1935.
The identity of Prunus lanata M. & B. Ibid. 254, 1935.

BUSH, B. F. AND CAMERON MANN—Supplement to the flora of Jackson County, Missouri. Independence, Mo. 1885.
MACKENZIE, K. K. AND B. F. BUSH—The Lespedezas of Missouri. Trans. Acad. Sci. St. Louis **12**:11-19, 1902.
———New plants from Missouri. Ibid. **12**:80-89, 1902.
———New plants from Missouri. Ann. Rept. Mo. Bot. Gard. **16**:102-108, 1905.

ARNOLD ARBORETUM,
JAMAICA PLAIN, MASS.

The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 18 JANUARY, 1937 No. 1

Studies on the Muscles of the Pelvic Appendage in Birds[1]

George Elford Hudson

TABLE OF CONTENTS

Introduction 2
Material and methods 3
Historical 7
Review of the muscles of the pelvic appendage 11
Ilio-trochantericus posterior 11
Ilio-trochantericus anterior 11
Ilio-trochantericus medius 12
Glutaeus medius et minimus 13
Iliacus 14
Ambiens 15
Sartorius 16
Ilio-tibialis 17
Femori-tibialis 19
Piriformis 21
Semitendinosus 22
Semimebranosus 24
Biceps femoris 25
Ischio-femoralis 26
Obturator internus 26
Obturator externus 27
Adductor longus et brevis 28
Tibialis anterior 29
Extensor digitorum longus 30
Peronaeus longus 33
Peronaeus brevis 34
Gastrocnemius 35
Plantaris 37
Flexor perforatus digiti II 39
Flexor perforatus digiti III 41
Flexor perforatus digiti IV 42
Flexor perforans et perforatus digiti II 44
Flexor perforans et perforatus digiti III 45
Flexor digitorum longus 46
Flexor hallucis longus 49
Popliteus 50
Extensor hallucis longus 51
Extensor proprius digiti III 53
Extensor brevis digiti II 53
Extensor brevis digiti IV 54
Abductor digiti II 55
Flexor hallucis brevis 55
Adductor digiti II 57
Lumbricalis 57
Adductor digiti IV 58
Abductor digiti IV 58
A proposed revision of Garrod's myological formula 59
A synopsis of the outstanding modifications of the muscles of the pelvic limb in the various species of birds studied 63
Order Gaviiformes 63
Order Colymbiformes 63
Order Pelecaniformes, Suborder Pelecani 64
Order Pelecaniformes, Suborder Fregatae 64
Order Ciconiiformes, Suborder Ardeae 65
Order Anseriformes, Suborder Anseres 65
Order Falconiformes, Suborder Cathartae 66
Order Falconiformes, Suborder Falcones 66
Order Galliformes, Suborder Galli 68
Order Gruiformes, Suborder Grues 69
Order Charadriiformes, Suborder Charadrii 70
Order Charadriiformes, Suborder Lari 70
Order Charadriiformes, Suborder Alcae 71
Order Columbiformes, Suborder Columbae 71
Order Cuculiformes, Suborder Cuculi 72
Order Strigiformes 72
Order Caprimulgiformes, Suborder Caprimulgi 73
Order Micropodiiformes, Suborder Micropodii 74
Order Piciformes, Suborder Pici 74
Order Passeriformes 75
Summary and conclusion 76
References 79
List of abbreviations 81
Plates 83

1 Studies from the Zoological Laboratory, University of Nebraska, No. 189.

Introduction

The purpose of this investigation was to examine the musculature of the pelvic appendage in at least one representative species of as many of the North American orders of birds as possible, and to elucidate the structural modifications of the various muscles, especially in so far as these might be of taxonomic significance. Of the twenty orders recognized in the fourth (1931) edition of the American Ornithologists' Union Checklist, representatives of sixteen were studied, those not available being the Procellariiformes, Psittaciformes, Trogoniformes, and Coraciiformes. The work was done during the six year period 1930-36 at the University of Nebraska.

Gadow (1891, p. 91) states that the literature dealing with bird muscles is extremely voluminous. His bibliography of avian myology contains 139 titles, including, as he states, the more important works. However many of them deal with muscles only in a brief and incidental way. Papers of broad scope which form really significant contributions to the subject are very scarce. Since the appearance of Gadow's comprehensive work very little has been added on the muscles of the pelvic extremity.

In America the only works of importance that have appeared are by Shufeldt (1886, 1890) and Burt (1930).

The terminology of bird muscles is in a state of chaos and from this standpoint Gadow's work (1891) added to the confusion since he renamed many of them on the doubtful basis of origin and insertion. Subsequently the Basle Nomina Anatomica (BNA) has appeared (1895) and is serving more and more as a great stabilizer of anatomical nomenclature.

In this work the BNA terminology has been adopted in so far as a knowledge of homologies would permit. Gadow's work has been used as the sole basis for this interpretation of homologies since it is the most authoritative work on the subject. His names have been retained for all muscles of unknown homology. The names of nineteen of the forty-one muscles of the pelvic appendage have been brought into conformity with the BNA. These names were taken from the work by Eycleshymer (1917) in which the complete BNA nomenclature is given.

The complete synonymy of each muscle is given by Gadow (1891), and Shufeldt (1890) has transcribed Gadow's synonymy into his work. Both of these works are readily accessible, hence complete synonymies are omitted from this treatise.

Practically the only comprehensive work on bird muscles available in English is that of Shufeldt (1890), but this, although important as a pioneer contribution, is deficient in many respects. As with many early writers on the subject, Shufeldt used a terminology of his own, and in addition the part

of his work dealing with the pelvic appendage of the raven contains minor mistakes of detail; moreover, three muscles of this region were entirely overlooked, no doubt because of their small size.

The illustrations of cross sections of the leg are believed to be a distinct advance over previous methods of delineation since they give a clearer conception of the disposition of the various muscles than can be obtained in any other way. This method has been extensively employed in human anatomy but apparently has never before been used to illustrate works on the musculature of birds.

The scientific and vernacular names of birds are those of the fourth (1931) edition of the American Ornithologists' Union Checklist, except for the fact that in general no cognizance is taken of sub-species, such determinations being of no value in an investigation of this type.

The writer wishes to acknowledge his indebtedness to the late Dr. Robert H. Wolcott of the University of Nebraska, under whom this investigation was first begun; to Dr. I. H. Blake of the same institution for many helpful suggestions during the preparation of this paper; to the Department of Zoology of the University of Nebraska for furnishing facilities for preserving and storing specimens and preparing the cross sections, and also for purchasing a number of specimens of forms that the writer was unable to obtain. The following persons also generously provided specimens: Dr. H. W. Manter and Prof. Myron H. Swenk of the University of Nebraska; Mr. A. M. Brooking of the Hastings Museum, Hastings, Nebraska; Major Allan Brooks of Okanagan Landing, British Columbia; Capt. H. L. Harllee of Florence, South Carolina; and Dr. Alden H. Miller of the Museum of Vertebrate Zoology of the University of California. Especial credit is due my wife for preparing a written translation of all of Gadow's work (1891) that deals with the appendicular muscles of birds.

Material and Methods

Soon after the specimens were killed most of the down and contour feathers were removed to allow the preservative to reach the skin. The bases of the flight feathers were left intact. Specimens were injected with a solution of one part commercial (40%) formalin to eight parts of water, then immersed in a vat of the same liquid. Thorough injection of all parts of the body is necessary, since mere evisceration and immersion in the liquid is not adequate for perfect preservation. When the latter method is used it may be many days before the formalin penetrates to the center of the large muscles, and during the interim the autolytic enzymes in the tissues bring about a partial digestion which so weakens them that satisfactory dissection of small structures becomes very difficult. Specimens were labeled with small wooden tags bearing catalogue numbers and stored in large crocks. A few drops of phenol were added to each container to prevent fungus growth. This compound, however, has the disadvantage of slowly decalcifying the skeletal parts and it is probable that toluene would prove better for this purpose. Specimens were prepared for study by partial dissection and washing in running

water for several days in order to remove most of the formalin. They were then transferred to a mixture of 50% alcohol and a little glycerine.

In the preparation of cross sections the legs (after being fixed in formalin) were passed through the series of alcohols up to 70%, then placed in Von Ebner's fluid and left for several weeks. After the bones were flexible the legs were cut into several pieces and returned to the same liquid where they remained until decalcification was complete. After this they were rinsed in 70% alcohol and placed in a second bath of this liquid containing sodium bicarbonate, and left overnight. This neutralized the remaining acid. Next the specimens were passed up through the series of alcohols and completely dehydrated. At this point they were cut into pieces of convenient size for sectioning. Absolute alcohol was followed by several changes of one-half absolute alcohol and one-half ether. From this they were transferred to a thin solution of celloidin and left for several weeks. The celloidin was gradually thickened by addition and evaporation. Best results were obtained, especially with large specimens, when infiltration occurred gradually over a period of several months; however, satisfactory sections were obtained with smaller specimens by the rapid ether-boiling method of infiltration (Guyer, 1930, p. 66) which requires only a few hours. After the celloidin was very thick it was transferred, together with the tissues, to small stender dishes. By loosening the top, evaporation was hastened so that after a few days the surface of the celloidin began to gel. Chloroform was then added and in a day or two the block was completely hardened. Blocks were then cut out, mounted and sectioned, or stored temporarily in 85% alcohol. Sections were cut from 30 to about 100 microns in thickness. For study they were stained and mounted in balsam in the usual manner.

The illustrations of cross sections were prepared by projecting the mounted sections in a micro-projection apparatus or in an ordinary lantern slide machine in the case of large sections. These were traced in pencil and later the sections were studied in detail under a low power binocular microscope before the drawings were inked. In the cross section drawings muscle tissue is represented diagrammatically by cross-hatching, since histological detail has no bearing on this investigation.

The various other illustrations were drawn either from projected photographic negatives or on the basis of careful measurements. The attachments on the bones were determined as follows: the various bones of the pelvic limb were separated so that the origins and insertions of the muscles remained intact. Each bone or major division of the leg was then worked out separately. The muscles were allowed to become partly dry, and all fat, connective tissue, etc., was carefully removed so as to isolate the sharply delimited muscle attachments. The part of the muscle next to the bone was painted with carbon ink and after drying the muscle was pulled away, leaving the exact outline of its attachment on the bone.

Small specimens were dissected with the aid of a low power binocular microscope.

List of Specimens Examined

Order Gaviiformes.
Family *Gaviidae.*
Common loon *(Gavia immer)* ---------- 1.

Order Colymbiformes.
Family *Colymbidae.*
Eared grebe *(Colymbus nigricollis californicus)* ---------- 1.

Order Pelecaniformes.
Suborder Pelecani.
Family *Sulidae.*
Brewster's booby *(Sula brewsteri)* ---------- 1.

Suborder Fregatae.
Family *Fregatidae.*
Man-o'-war-bird *(Fregata magnificens)* ---------- 1.

Order Ciconiiformes.
Suborder Ardeae.
Family *Ardeidae.*
Great blue heron *(Ardea herodias)* ---------- 1.
Green heron *(Butorides virescens)* ---------- 1.

Order Anseriformes.
Suborder Anseres.
Family *Anatidae.*
Lesser snow goose *(Chen hyperborea)* ---------- 1.

Order Falconiformes.
Suborder Cathartae.
Family *Cathartidae.*
Turkey vulture *(Cathartes aura septentrionalis)* ---------- 1.

Suborder Falcones.
Family *Accipitriidae.*
Mississippi Kite *(Ictinia misisippiensis)* ---------- 1.
Cooper's hawk *(Accipiter cooperi)* ---------- 1.
Red-tailed hawk *(Buteo borealis)* ---------- 2.
Swainson's hawk *(Buteo swainsoni)* ---------- 1.
Marsh hawk *(Circus hudsonius)* ---------- 1.

Family *Falconidae.*
Prairie falcon *(Falco mexicanus)* ---------- 1.
Duck hawk *(Falco peregrinus anatum)* ---------- 1.
Sparrow hawk *(Falco sparverius)* ---------- 3.

Order Galliformes.
Suborder Galli.
Family *Tetraonidae.*
Sharp-tailed grouse *(Pedioecetes phasianellus)* ---------- 1.

Family *Perdicidae.*
Bob-white *(Colinus virginianus)* ---------- 2.

Order Gruiformes.
Suborder Grues.
Family *Gruidae.*
Little brown crane *(Grus canadensis)* ---------- 1.

Family *Rallidae.*
American coot *(Fulica americana)* ---------- 2.

Order CHARADRIIFORMES.
Suborder CHARADRII.
Family *Scolopacidae.*
Greater yellowlegs *(Totanus melanoleucus)* ---------- 1.
Lesser yellowlegs *(Totanus flavipes)* ---------- 1.

Suborder LARI.
Family *Laridae.*
Franklin's gull *(Larus pipixcan)* ---------- 1.

Suborder ALCAE.
Family *Alcidae.*
California murre *(Uria aalge californica)* ---------- 1.

Order COLUMBIFORMES.
Suborder COLUMBAE.
Family *Columbidae.*
Mourning dove *(Zenaidura macroura)* ---------- 2.

Order CUCULIFORMES.
Suborder CUCULI.
Family *Cuculidae.*
Yellow-billed cuckoo *(Coccyzus americanus)* ---------- 2.

Order STRIGIFORMES.
Family *Strigidae.*
Screech owl *(Otus asio)* ---------- 2.
Great horned owl *(Bubo virginianus)* ---------- 2.

Order CAPRIMULGIFORMES.
Suborder CAPRIMULGI.
Family *Caprimulgidae.*
Nighthawk *(Chordeiles minor)* ---------- 2.

Order MICROPODIIFORMES.
Suborder MICROPODII.
Family *Micropodidae.*
Chimney swift *(Chaetura pelagica)* ---------- 2.

Order PICIFORMES.
Suborder PICI.
Family *Picidae.*
Flicker *(Colaptes auratus)* ---------- 2.
Hairy woodpecker *(Dryobates villosus)* ---------- 1.

Order PASSERIFORMES.
Suborder TYRANNI.
Family *Tyrannidae.*
Eastern kingbird *(Tyrannus tyrannus)* ---------- 2.

Suborder PASSERES.
Family *Corvidae.*
American raven *(Corvus corax sinuatus)* ---------- 1.
Eastern crow *(Corvus brachyrhynchos)* ---------- 40.

In addition numerous other species were examined in order to check certain specific points.

Historical

Many of the papers on avian myology deal with descriptions of single forms. Only a few approach the subject from a comparative viewpoint. The following is a brief review of some of the outstanding papers dealing with the pelvic musculature of birds.

Vicq d'Azyr published important papers on the anatomy of birds (1772-1778) which give detailed descriptions of muscles based on the investigation of a large series of forms. It is deficient in specific details. This writer and Cuvier introduced the method of naming muscles according to the origin and insertion.

The beginning of the nineteenth century marked a great increase in the production of works on the myology of birds. This was the period when comparative anatomy became popular and many of the works dealing with bird muscles were concerned mainly with comparisons of birds with other vertebrate classes in an effort to determine homologies.

In 1810 Tiedemann published on the anatomy and natural history of birds, giving fairly accurate descriptions of the muscles in general and an exhaustive consideration of the literature.

Meckel (1825) described the muscles of numerous birds in his System der vergleichenden Anatomie. He also wrote a comparative account of the muscles in several genera of "Ratitae" (1830).

Owen (1835) wrote an article on birds in Todd's Cyclopaedia of Anatomy and Physiology, giving general descriptions of the muscles. This was followed by a classical work on the anatomy of *Apteryx australis* (1849).

Sundevall was one of the first to use myological characters in furthering avian taxonomy. In 1851 he published an important paper on the homologies of the muscles of the extremities. Sundevall questioned the old conception of the use of the ambiens, i.e., that it functions to maintain the sleeping bird on its perch by producing a tension on the perforating flexor muscles when the legs are folded up under the body. He set off the Passeriformes (including *Upupa*) from all other birds since they alone lack any connection between the two deep flexor tendons of the foot.

Nitsch-Giebel published several important papers during the period 1857-1863. His work on the anatomy of parrots (1862) is based on an examination of eleven genera and thirty-two species.

Klemm (1864) contributed an account of the musculature of ravens based on an investigation of six species.

Haughton published several papers (1865-1868) dealing mainly with various genera of the "Ratitae."

Alix wrote several important works (1867-1876) which give excellent descriptions of the muscles in general, together with comparisons of bird muscles with those of reptiles and mammals. His work on the locomotor apparatus of birds (1874) gives exhaustive literature references.

Coues was one of the few American ornithologists to publish on myology. He wrote a paper (1867) on the osteology and myology of *Colymbus torquatus* (=*Gavia immer*).

In 1869 Selenka published the first part of the bird volume for Bronn's Klassen und Ordnungen des Thier-Reichs. This great work was completed by Gadow many years later (1891).

Watson (1869) wrote on the mechanism of perching in birds. By careful study and experimentation he proved that the ambiens muscle (called *rectus femoris* by him) is not responsible for holding the sleeping bird on its perch as was formerly believed. Birds in which the tendon of this muscle had been cut retained unimpaired their capacity for perching. This old idea concerning the function of the ambiens apparently started with Owen. Many subsequent authors accepted this but Sundevall pointed out that the muscle in question is absent in many birds that perch and is present in most swimming birds. This latter author, however, did not base his conclusions on experimental evidence as did Watson.

Probably the most outstanding work by a single investigator was that of Garrod who published a number of papers on bird muscles in the Proceedings of the Zoological Society of London during the period 1872-1877. As Prosector of the Zoological Society he had unprecedented opportunity for dissecting large numbers of birds of great taxonomic diversity. His attention was directed chiefly to a comparative study of the thigh muscles. He found that five muscles of this region are present in many birds and absent in others. These are the femoro-caudal (piriformis, *Pars caudifemoralis*), the accessory femoro-caudal (piriformis, *Pars ilio-femoralis*), the semitendinosus, the accessory semitendinosus, and the ambiens. The first four of these were designated by the letters A, B, X, and Y, respectively. On this basis myological formulae were worked out for the various higher groups of birds. Garrod believed that the ambiens muscle was of greatest taxonomic significance and he divided the class Aves into two subclasses, the *Homalogonatae* (ambiens present) and the *Anomalogonatae* (ambiens absent). This division is considered artificial since it is based mainly on a single character and it has not been adopted. However, Garrod's myological formulae (various combinations of A-B, X-Y, and ambiens) have been extensively used by taxonomists as aids in characterizing the higher groups of birds. Although Garrod's principal work was on the thigh he also studied the tendons of the two deep flexor muscles of the foot (flexor hallucis longus and flexor digitorum longus), and determined in which birds they are connected by a vinculum and in which this is lacking. In addition he worked out the various modifications of the vinculum in the birds possessing it. Garrod's work is well summarized by Forbes (1881).

DeMan (1873) in a comparative myological and neurological study in amphibia and birds gives accurate descriptions of the limb muscles in several genera of birds. In addition the innervations and homologies are given, many of the latter being reported for the first time.

After the untimely death of Garrod, Forbes was made Prosector of the

Zoological Society of London. He published several papers on avian anatomy, the most important of which was on the Tubinares (1882) collected during the voyage of H. M. S. Challenger. This contains a section on myology.

Gadow made several very important contributions to the subject. One of his earlier papers was on the comparative myology of the pelvic extremity in the "Ratitae" (1880). He paid particular attention to homologies of the avian muscles in comparison with those of other vertebrates. In determining homologies he placed great emphasis on innervations, considering these the surest guide to a correct interpretation. His great work on bird anatomy in Bronn's Thier-Reich (1891) is the most exhaustive and elaborate volume ever published on the subject. The section on myology contains 234 pages and seventeen plates, fourteen of the latter being colored. Seventy-five pages and ten plates deal with the muscles of the pelvic limb. In addition there is a bibliography of 139 titles. This work is monographic in scope and the complete synonymy is given for each muscle, together with descriptions, innervations, and homologies.

Although Gadow's work is on the whole very accurate, he made the mistake in certain cases of working out the muscles in a few genera within a family or order and on this incomplete basis making sweeping statements about the entire group. For example, he states (1891, p. 142) that in the Columbidae all three of the iliotrochantericus muscles are grown together; however, in *Zenaidura macroura* all three are clearly defined. Again, he says (1891, p. 186) that the plantaris muscle is wholly lacking in all diurnal and nocturnal birds of prey; yet in several species of *Falco* (all those examined) it is powerfully developed—also present in *Cathartes*.

Haswell (1880, 1883), Sabatier (1880), and Weldon (1883) published papers of importance.

Shufeldt (1886) wrote an extensive paper on the anatomy of the roadrunner *(Geococcyx californianus)*. This and his work on the raven (1890) are the most important that have appeared in America. Both were published in England but the work was done in the United States. The Myology of the Raven is the most voluminous single contribution ever made on the muscular system in birds. It contains 343 pages and 76 figures in the text. One hundred two pages and 29 figures are concerned with the pelvic limb. There is a bibliography of 144 titles. This work is important as a pioneer contribution in America but has several serious drawbacks. It was written while the author was in New Mexico without access to the literature; furthermore, many of the muscle names are of his own invention. Some are based on a misinterpretation of homologies, others are entirely without precedent and are imperfectly applicable even to the raven—the *Flexor perforatus annularis primus pedis*, for example. This work was designed as a guide to the study of the muscular system in birds and is only casually concerned with comparisons between the various bird groups. Three muscles of the pelvic limb were overlooked in the raven, no doubt because of their small size. These are the iliacus, the ilio-trochantericus medius, and the flexor hallucis

brevis. Other errors of detail are numerous. The complete synonymy of Gadow is given for each muscle.

Marshall (1905) published one of the few American papers on the subject. This, treating the anatomy of the poor-will *(Phalaenoptilus nuttalli)*, is very inaccurate as far as the pelvic muscles are concerned. An attempt was made to use the terminology of Gadow and, as the author indicates, her findings fail to agree with his in many respects. These disparaties will be considered in the order in which they appear. Marshall claims that the iliotrochantericus muscle is a single unit and does not show the division into three muscles as given by Gadow. This is probably an error since I have found this muscle single only in *Sula*, all others, including *Chordeiles minor*, having at least two. The *M. caud-ilio-flexorius* (semitendinosus) is said to show "great deviation from Gadow's description", in spite of the fact that her description is typical of this muscle (as described by Gadow) when both the muscle proper and the "accessorius" are well developed; however, she gives the origin as coming from the posterior border of the ischium. This is probably an error also since the origin, although in some cases reaching down onto the ischium, is principally from the ilium and caudal vertebrae. It is stated that the *Pars caudalis* of the *M. caud-ilio-femoralis* (piriformis) does not agree in origin with Gadow's description. This criticism is well founded, for Gadow gives the origin of this muscle in Carinates as being from the transverse processes of several caudal vertebrae, whereas in many it is from the coccyx only. The *M. pub-ischio-femoralis* (Adductor longus et brevis) is said to consist of only one part. This is probably an error for in most birds (including *Chordeiles minor)* it is made up of a *Pars interna* and a *Pars externa*. The obturator muscle is said to vary considerably from Gadow's description and to spring from the edges of the obturator foramen, thus agreeing in some points with his *Mm. accessorii m. obturatoris* (obturator externus). From this it is evident that the entire belly of the obturator internus (which lies on the inside of the pelvis) was overlooked! A muscle that the author was unable to identify is described under the letter "X" and the statement is made that Gadow did not describe such a muscle. The description given, however, is that of a typically developed *M. femori-tibialis internus* of Gadow. The most serious error in this work is the fact that *Phalaenoptilus* is given the myological formula AY as contrasted with AXY in several other genera of Caprimulgidae. Actually the formula is identical with the others, the semitendinosus (X) being present in all. It is interesting to note that this work by Marshall was reviewed in the Ibis (1906, p. 591) and rated as an "exhaustive memoir"!

Burt (1930) briefly described the muscles of the pileated woodpecker *(Ceophloeus pileatus)*. Unfortunately the nomenclature of Shufeldt was used. It is stated that an attempt was made to follow the BNA as closely as possible; however, Shufeldt's names are closely followed, the changes being only minor ones in spelling and the transposition of the component words. Burt followed Shufeldt in overlooking the *M. iliacus* (which is very weakly developed in woodpeckers). In addition he overlooked the extensor proprius digiti III and the abductor digiti IV.

A Systematic Review of all the Muscles Known to Occur in the Pelvic Limb of Birds

MM. ILIO-TROCHANTERICI

This muscle complex is subdivided into three parts all of which are independently developed in the crow and raven. They all arise broad and fleshy from the outer side of the pre-acetabular ilium and insert by rather broad and flat tendons on the external surface of the trochanter of the femur.

M. ILIO-TROCHANTERICUS POSTERIOR (Il. troc. post.)

Gluteus medius—Shufeldt (1890, p. 160).
M. ilio-trochantericus posterior—Gadow (1891, p. 141).

Description (for the crow and raven).—This is by far the largest of the muscles passing from the ilium to the femur. It arises fleshy from almost the entire lateral surface of the pre-acetabular ilium (Figs. 2, 8). Its fibers converge rapidly as it passes postero-laterally, to form a broad and strong tendon which glides over the external surface of the proximal end of the femur to the insertion on the middle and outer aspect of the trochanter. This point of insertion extends farther proximally than any other muscle attachment on the femur (Fig. 8). The Il. troc. post. is almost completely covered laterally by the Il. tib., especially by the proximal aponeurosis of that muscle.

Action.—Rotates the femur forward and inward.

Homology.—According to Gadow (1891, p. 139) the *Mm. il. troc.* must be looked upon as structures peculiar to birds and possessing no homologues in man, since the human ilium corresponds to only the part of the avian ilium which lies immediately around the acetabulum and somewhat posterior to this. The pre-acetabular ilium of birds is peculiar to them; accordingly, the *Mm. il. troc.* do not correspond to the gluteal muscles of mammals as Shufeldt (1890, p. 160) and other writers have considered.

Comparison.—This muscle is present in all the birds examined and is subject to no significant modifications. Its shape is greatly modified by the various shapes of the pre-acetabular ilium. Ordinarily the Il. troc. post. is much larger than the other two Il. troc. muscles; however, in *Colymbus* it is much smaller than the Il. troc. ant. It is long and narrow in *Gavia, Colymbus,* and *Chordeiles,* conforming with the narrow pre-acetabular ilium. On the other hand it is quite short in *Coccyzus, Colaptes,* and *Dryobates.* The insertion in most forms is similar to that in the crow but in *Gavia* it is on the extreme anterior border of the trochanter, quite similar to that in *Larus.* In *Sula* there is only one Il. troc. muscle which possibly represents a fusion of the usual three. Gadow (1891, p. 142) has reported this condition in *Sula bassana* (= *Morus bassanus*).

M. ILIO-TROCHANTERICUS ANTERIOR (Il. troc. ant.)

Gluteus minimus—Shufeldt (1890, p. 163).
M. ilio-trochantericus anterior—Gadow (1891, p. 142).

Description (for the crow and raven).—This is the medium-sized Il. troc. muscle. It arises semitendinous from a narrow line on the ventral edge of the ilium, lying between the origins of the sartorius in front and the

Il. troc. med. behind (Figs. 2, 3, 8). The rather thin triangular muscle passes postero-laterally, parallel to the Il. troc. post., to its insertion on the external surface of the trochanter, just beyond the point of insertion of the Il. troc. med. and between the heads of the Fem. tib. ext. and the Fem. tib. med. (Fig. 8). Externally this muscle is exposed throughout most of its extent upon the removal of the Il. tib. It does not take part of its origin from the last rib as claimed by Shufeldt (1890, p. 166), but arises from the ilium only. On its dorsal surface the belly is rather intimately connected with the Il. troc.. post.

Action.—Accessory to the powerful Il. troc. post. in rotating the femur forward and inward.

Homology.—Peculiar to birds (Gadow, 1891, p. 139).

Comparison.—The Il. troc. ant. shows no very important variations and is present in all except *Sula*. In this form it is probably fused with the other Il. troc. muscles; at any rate it is not present as an independent muscle. In most forms the origin is from almost the entire ventral edge of the pre-acetabular ilium. This is the case in *Falco, Buteo, Chen, Chordeiles, Ardea, Fulica, Grus,* and *Totanus*. In *Larus* and *Fregata* it arises from only the middle portion of the ventral edge of the pre-acetabular ilium. The following closely resemble the crow: *Uria, Zenaidura, Pedioecetes, Colinus, Chaetura, Coccyzus, Colaptes, Dryobates,* and *Tyrannus*. *Bubo* and *Otus* are similar to the crow except that the origin is from a somewhat greater portion of the ilium. In *Gavia* the Il. troc. ant. is fleshy throughout and is fully as large as the Il. troc. post. In *Colymbus* it is much larger than the latter. This does not confirm Gadow's statement (1891, p. 141) that the Il. troc. post. is always the most highly developed. However, in most birds the Il. troc. ant. is much smaller than the Il. troc. post.

M. ILIO-TROCHANTERICUS MEDIUS (Il. troc. med.)

Overlooked by Shufeldt (1890) in the raven.
M. ilio-trochantericus medius—Gadow (1891, p. 142).

Description (for the crow and raven).—This is by far the smallest of the three Il. troc. muscles. It arises fleshy from a small area near the ventral edge of the ilium, just in front of the acetabulum (Figs. 3, 8). Immediately below its origin lies that of the Iliacus. From its point of origin this small muscle extends laterally and somewhat posteriorly to its insertion on the antero-lateral border of the trochanter, between the points of insertion of the Il. troc. post. and the Il. troc. ant. (Fig. 8).

Shufeldt (1890) entirely overlooked this muscle in the raven in which it is clearly evident just as in the crow.

Action.—Aids the two other Il. troc. muscles in rotating the femur forward and inward.

Homology.—Peculiar to birds (Gadow, 1891, p. 139).

Comparison.—In many birds the Il. troc. med. is absent, or at least it is not independently developed. In such cases it may be fused with the Il. troc. ant. but for all practical purposes may be considered absent.

The following is a synopsis of the occurrence of this muscle in the birds examined.

Absent		Present
Sula	*Fulica*	*Gavia*
Fregata	*Totanus*	*Colymbus*
Ardea	*Uria*	*Cathartes*
Butorides	*Coccyzus*	*Pedioecetes*
Chen	*Otus*	*Colinus*
Buteo	*Bubo*	*Larus*
Falco	*Chordeiles*	*Zenaidura*
Grus	*Chaetura*	*Colaptes*
		Dryobates
		Tyrannus
		Corvus

Gadow (1891, p. 142) states that all three of the Il. troc. muscles are grown together in the Columbidae. Nevertheless I find them clearly separable in *Zenaidura* and the domestic pigeon *(Columba livia)*.

Garrod (1874) did not include this muscle in his myological formula. As regards presence or absence (which was the feature emphasized by Garrod) it shows a variability in the different orders of birds comparable to that shown by the five muscles in his formula. I believe that it could well be included. Since Garrod has designated four of his formula muscles by the letters A, B, and X, Y, the Il. troc. med. could be given the letter C.

M. GLUTAEUS MEDIUS ET MINIMUS (Glut. med. et min.)

M. ilio-femoralis externus—Gadow (1891, p. 143).

Description (for the great horned owl—*Bubo virginianus)*.—Arises from the ventral edge of the lateral ridge of the ilium directly opposite the acetabulum. The distal half of this small and flat muscle is a thin tendinous sheet which passes over the posterior half of the trochanter, and inserts on a transverse line just proximal to the tendon of the Isch. fem.; in fact, the tendons of these two muscles are very intimately grown together at right angles to each other. The Glut. med. et min. is covered laterally by the Il. tib. and the Bic. fem.

This muscle is figured for the bob-white *(Colinus virginianus)* on Pl. 24, Fig. 64.

Action.—Very weak—but tends to abduct the femur.

Homology.—Gadow (1891, p. 209) gives the *M. ilio-femoralis externus* as homologous to the *M. glutaeus medius et minimus* of man.

Comparison.—The following is a synopsis of the forms in which the Glut. med. et min. is apparently absent and those in which it is definitely present:

Absent	Present	
Colymbus	*Gavia*	*Pedioecetes*
Zenaidura	*Sula*	*Colinus*
Coccyzus	*Fregata*	*Grus*
Chordeiles	*Ardea*	*Fulica*
Chaetura	*Chen*	*Totanus*
Colaptes	*Butorides*	*Larus*
Dryobates	*Buteo*	*Uria*
Tyrannus	*Falco*	*Otus*
Corvus		*Bubo*

It is very difficult in the case of small birds to determine whether this little muscle is absent or simply rudimentary. Gadow (1891, p. 144) indicates that in some cases it is completely fused with the posterior margin of the Il. troc. post. However, as has already been pointed out in connection with the Il. troc. med., such a completely fused muscle is for all practical considerations absent, especially if the innervation fails to provide a definite basis for determination as Gadow indicates is the case with the Glut. med. et min.

It is possible that a careful study of all the orders and families of birds would provide evidence to justify the use of this muscle in myological formulae. In the present study it was found to be absent in representatives of seven out of fifteen orders. The letter "D" would be suitable for designating this muscle in a myological formula.

The variations in structure of this muscle among the various groups of birds is slight. It is most strongly developed in *Buteo, Sula, Ardea,* and *Falco.* In the following the insertion is about as in *Bubo: Sula, Fregata, Ardea, Butorides, Buteo, Falco.* It is just in front of the middle of the tendon of the Isch. fem. in *Pedioecetes, Colinus, Grus,* and *Fulica.* The insertion is adjacent to the distal edge of the tendon of the Isch. fem. in *Chen, Totanus, Larus,* and *Uria.*

In *Gavia* the short tendon is quite distinct but the belly appears to be intimately fused with the Il. troc. post. It inserts farther proximally than in other forms—opposite the insertion of the Obt. int.

M. ILIACUS (Iliacus)

Overlooked by Shufeldt (1890) in the raven.
M. ilio-femoralis internus—Gadow (1891, p. 144).

Description (for the crow and raven).—This little muscle is fleshy throughout, and is the smallest of all the muscles associated with the thigh. It arises from the ventral border of the ilium, slightly in front of the acetabulum and immediately below the origin of the Il. troc. med. (Figs. 6, 8, 9). From this point it runs postero-laterally to its insertion on the medial side of the femoral shaft, between the head of the femur and the proximal end of the Fem. tib. int.

Shufeldt (1890) overlooked this little muscle entirely, although it has the same relative development in the crow and the raven. This is clearly evident in a specimen of the raven at hand.

Action.—Although extremely weak the *M. iliacus* aids in drawing the femur forward, at the same time adducting it. As pointed out by Gadow (1891, p. 144), this muscle acts as an Il. troc. on the medial side.

Homology.—Gadow (1891, p. 140) states that the *M. ilio-femoralis internus* of birds corresponds in origin, insertion, and innervation to the *M. iliacus* of man.

Comparison.—The iliacus is present in all the forms examined and is one of the most uniformly developed thigh muscles in birds. It is weakest in *Dryobates* and this probably accounts for the fact that Burt (1930) over-

looked it in woodpeckers. It is unusually short and broad in *Gavia* and *Colymbus*. *Fulica* and *Chordeiles* also have it strongly developed.

M. AMBIENS (Ambiens)

M. ambiens—Gadow (1891, p. 145).

Description (for Swainson's hawk—*Buteo swainsoni)*.—This muscle lies superficially on the medial surface of the thigh. It arises by a short flat tendon from the *Spina pubica*. The tendon unites below with the flat spindle-shaped belly which passes downward along the medial surface of the Fem. tib. (Figs. 46, 67). About two-thirds the way down the thigh the belly gives way to the long flat tendon which passes under the sartorius on the inner side of the knee region. Farther down it passes under the patellar tendon and around the front of the knee to the external side of the shank, where it perforates the proximal end of the belly of the F. p. et p. d. III. From here it passes inward and downward to the lateral surface of the fibula, and under the tendon of insertion of the Bic. fem. (which holds it firmly down against the deep flexor). Shortly below the insertion of the Bic. fem. the tendon of the *M. ambiens* serves as a head of origin for the Flex. per. d. II (Fig. 68). The *Mm. flex. per d. III* and *IV* are also rather intimately connected with this tendon, but the Flex. per d. II forms a direct continuation of it.

The tendon of insertion of the *M. ambiens* makes up about three-fifths of the total length of the muscle. It is not visible superficially beyond the point where it passes beneath the sartorius.

Action.—Aids in flexing the fore toes but more especially the second one.

Homology.—The *M. ambiens* is independently developed only in reptiles and birds. It is absent in the mammals Gadow (1891, p. 148).

Comparison.—This is one of the five "formula muscles" of Garrod. Its occurrence is as follows.

Absent	Present
Colymbus	*Gavia*
Ardea	*Sula*
Butorides	*Fregata*
Bubo	*Chen*
Otus	*Cathartes*
Chordeiles	*Buteo*
Chaetura	*Falco*
Colaptes	*Pedioecetes*
Dryobates	*Colinus*
Tyrannus	*Grus*
Corvus	*Fulica*
	Totanus
	Larus
	Uria
	Zenaidura
	Coccyzus

In *Gavia* the ambiens shows a very peculiar development: it is extremely broad and flat and arises tendinous from the *Spina pubica* and fleshy from the ventral edge of the pubis for a distance of about 20 mm. behind this. After passing beneath the broad sartorius muscle it narrows into a strong

tendon which passes abruptly toward the outside through a partly ossified loop on the postero-inner edge of the tibia, a little in front of the articulation with the femur. It passes *laterally* to the tendon of insertion of the Il. tib.

In *Chen* the origin is quite similar to that in *Gavia*. The origin is also partly fleshy in *Colinus, Grus, Fulica,* and *Totanus*.

Falco differs from all other forms studied in that the tendon of insertion passes *laterally* to the tendon of the Bic. fem.

This muscle is very strongly developed in *Fulica,* continuing fleshy almost to the knee. It is peculiar in showing a definite longitudinal division of the belly into two parts. This is especially evident on the medial surface. It is interesting to note that another member of the Rallidae, *Porzana carolina,* shows this condition also.

In *Colinus* the belly is very short and broad, extending only about halfway down the thigh.

The ambiens is present in *Uria* but is very weakly developed. Garrod (1874, p. 117) indicates that it is present in no genus of Alcidae. Gadow (1891, p. 146) also states that this muscle is completely missing in the Alcidae; however, on Plate XXV, which gives a synopsis of the presence and absence of Garrod's formula muscles in the various bird groups, he indicates *Uria* as having the ambiens muscle present. Nevertheless, in volume two of his work (Systematischer Theil) nothing is said about *Uria* having this muscle. Systematists have apparently overlooked Gadow's treatment of *Uria* (on Plate XXV) for Ridgway (1919, p. 701), in speaking of the Suborder Alcae, states that the ambiens is always absent.

This muscle is extremely small in *Uria* and might easily be overlooked. The minute tendon disappears on the fascia covering the inner side of the knee region. It does not pass the knee joint.

No important differences were noted in the mode of insertion of this muscle in the other birds examined.

M. SARTORIUS (Sar.)

Sartorius—Shufeldt (1890, p. 156)
M. ilio-tibialis internus s. sartorius—Gadow (1891, p. 149)

Description (for the crow and raven).—This is the most anterior of the thigh muscles. It originates fleshy from the antero-dorsal border of the ilium (Figs. 1, 8), and from the spinous process of the last free dorsal vertebra. The long strap-like belly extends downward to the antero-inner border of the knee region (Figs. 6, 18-22). Here it forms a half-tendinous insertion on a very narrow line on the antero-inner border of the proximal end of the tibial head (Fig. 12). In addition it inserts on the antero-inner side of the patellar tendon, as well as to a limited extent on the fascia covering the anterior side of the knee region.

Throughout most of its extent the *M. sartorius* is rather intimately connected with the anterior edge of the Il. tib.

Action.—Pulls the thigh forward and upward, at the same time extending the shank.

Homology.—Gadow (1891, p. 150) states that the *M. ilio-tibialis internus* corresponds to the *M. sartorius* of mammals.

Comparison.—The sartorius is present in all the birds examined and is subject to no great modifications. In most forms it inserts mainly on the medial edge of the patellar tendon, and also to a limited extent on the *Caput tibiae*. The origin is far more variable than the insertion. In the following the sartorius is throughout very similar to that in the crow: *Zenaidura, Coccyzus, Chordeiles, Chaetura, Tyrannus. Gavia, Colaptes,* and *Dryobates* differ in that the origin extends much farther back along the ventral edge of the ilium, the muscle being consequently much broader than usual. *Larus* and *Totanus* are similar to the crow except that the insertion is mostly on the patellar tendon.

The origin is exclusively from the ventral edge of the ilium in *Bubo* and *Otus*. It is from the anterior edge of the ilium only in *Fregata, Pedioecetes, Colinus, Grus, Buteo,* and *Falco*. In the following it is from the posterior dorsal vertebrae and the antero-dorsal edge of the ilium: *Ardea, Butorides, Chen, Fulica,* and *Uria*. The origin in *Sula* is from the dorsal crest of the synsacrum only.

The insertion is very peculiar in *Gavia* and *Colymbus*, being directly on the bone on the inner side of the proximal end of the tibia. The area of attachment is very sharply delimited.

M. ILIO-TIBIALIS (Il. tib.)

Gluteus primus—Shufeldt (1890, p. 158).
M. ilio-tibialis—Gadow (1891, p. 151)

Description (for the crow and raven).—The Il. tib. is the most superficial muscle of the thigh. It is broad and triangular, and covers several of the deeper muscles of this region (Figs. 1, 18-22). The origin is from a long but very narrow line on the dorso-lateral ridge of the ilium, extending from the *M. sartorius* in front to the *M. semitendinosus* behind (Fig. 8). This origin is aponeurotic, except for the extreme posterior portion which is partly fleshy. Along its anterior margin this muscle is rather intimately connected with the sartorius and the middle region is strongly fused with the underlying Fem. tib. Distally this muscle contributes, together with the Fem. tib., to the formation of the patellar tendon, which encloses the sesamoid and passes farther downward to insert on a long but very narrow line on the proximal end of the anterior crest of the head of the tibia. (Fig. 12).

Although in the crow and raven the Il. tib. forms a single and undivided sheet, there are three clearly discernible regions, at least on the distal half. These are: (1) an anterior fleshy part, probably corresponding to Gadow's (1891, p. 152) Il. tib. ant.; (2) a middle mostly aponeurotic portion representing, probably, the Il. tib. med. or *tensor fasciae;* and, (3) a posterior fleshy portion representing, no doubt, the Il. tib. post. or *gluteus posterior.*

Action.—Aids the Fem. tib. in extending the shank. The posterior part also probably tends to draw the leg away from the body.

Homology.—According to Gadow (1891, p. 209) the Il. tib. ant. has no

homologue in man, but the Il. tib. med. corresponds to the *M. tensor fasciae latae,* and the *Il. tib. post.* to the *M. glutaeus maximus.* These latter names should, therefore, be used for the subdivisions to which they apply; however, it seems best to retain the name *M. ilio-tibialis* for the combined muscle in birds.

Comparison.—The ilio-tibialis is present in all forms studied but varies greatly in structure in the different taxonomic groups. In the following it closely resembles the condition in the crow: *Butorides, Pedioecetes, Colinus, Grus, Fulica, Totanus, Zenaidura.* In *Ardea, Chen,* and *Larus* it differs in overlapping much less of the biceps femoris at the proximal end.

The middle portion of this muscle is aponeurotic for the entire length in *Coccyzus, Colaptes,* and *Dryobates;* as a result the fleshy anterior and posterior portions are not contiguous at any point.

The origin is from the acetabular and pre-acetabular ilium in *Buteo, Falco, Bubo,* and *Otus,* the muscle overlapping no part of the Bic. fem. although the tendons of origin of the two are firmly fused proximally. In these birds the origin is from both the dorsal and anteroventral portions of the ilium. This ventral connection is tendinous in the hawks and fleshy in the owls. In *Sula* and *Uria* also the Il. tib. is confined to the acetabular and pre-acetabular ilium, but overlaps the front edge of the biceps.

Only the posterior portion is fleshy in *Chordeiles* and the rest of the muscle, if present at all, is represented only by a thin fascia-like sheet.

In the families Tyrannidae and Hirundinidae the post-acetabular portion of the Il. tib. is absent. This is true in spite of the fact that Garrod (1873, p. 630) states that the post-acetabular portion of this muscle (called *tensor fasciae* by him) is present in the Passeres (Passeriformes). Gadow (1891, p. 153) indicates the same thing. Apparently the absence of the post-acetabular portion in the Tyrannidae and Hirundinidae has never before been reported. All the other families of Passeriformes examined have the Il. tib. developed about as in the crow (with the post-acetabular portion well developed.

Species of Passeriformes examined:

Post-acetabular portion absent—	Tyrannidae—	*Sayornis phoebe.*
		Empidonax virescens.
		Myiarchus crinitus.
		Tyrannus tyrannus.
	Hirundinidae—	*Stelgidopteryx ruficollis serripennis.*
		Petrochelidon albifrons.
Post-acetabular portion present—	Alaudidae—	*Otocoris alpestris.*
	Corvidae—	*Corvus brachyrhynchos.*
		Corvus corax sinuatus.
	Paridae—	*Baeolophus bicolor.*
	Sittidae—	*Sitta carolinensis.*
	Certhiidae—	*Certhia familiaris americana.*
	Chamaeidae—	*Chamaea fasciata.*
	Cinclidae—	*Cinclus mexicanus unicolor.*
	Mimidae—	*Dumetella carolinensis.*

Turdidae—	*Turdus migratorius.*
Sylviidae—	*Polioptila caerulea.*
Motacillidae—	*Anthus spinoletta rubescens.*
Bombycillidae—	*Bombycilla cedrorum.*
Laniidae—	*Lanius ludovicianus.*
Sturnidae—	*Sturnus vulgaris.*
Vireonidae—	*Vireo belli.*
Compsothlypidae—	*Dendroica aestiva.*
Ploceidae—	*Passer domesticus.*
Icteridae—	*Sturnella neglecta.*
Thraupidae—	*Piranga rubra.*
Fringillidae—	*Richmondena cardinalis.*

This tends to confirm the recent tendency of taxonomists to place the Hirundinidae very closely following the Tyrannidae. The ilio-tibialis should be studied throughout the great series of perching birds in order to determine its taxonomic significance. It is not impossible that it might prove to be as important as the modifications of the syringeal muscles which at present serve as the basis for dividing the order Passeriformes into two suborders.

In *Chaetura* this muscle shows about the same condition as in *Tyrannus,* the post-acetabular portion being absent.

In *Fregata* the ilio-tibialis is greatly reduced, being very narrow and arising only from the acetabular ilium. Insertion is by a narrow fleshy ribbon on the femori-tibialis, about halfway down the thigh.

This muscle is very broad and strong in *Gavia,* arising almost entirely fleshy from a long line on the dorsal ridge of the ilium beginning well behind the ischiadic foramen and extending forward onto the last two free dorsal vertebrae.

In *Colymbus* it is divided into two fleshy portions which are widely separated at the proximal end. These converge but do not meet distally. The anterior head is ribbon-shaped and arises from the antero-dorsal edge of the ilium and the last free dorsal vertebra. The posterior head is very broad and originates from the entire lateral ridge of the post-acetabular ilium. In the wide gap between them these two bellies are connected only by a thin sheet of fascia at the proximal end but by a stronger aponeurotic sheet distally. The anterior part inserts on the lateral side of the long patellar crest in company with the femori-tibialis. The posterior part inserts partly on the patella but mostly on the perforating flexor muscles.

M. FEMORI-TIBIALIS (Fem. tib.)

Description (for the crow and raven).—Under the head of *M. femori-tibialis* Gadow (1891, p. 155) places all those muscles which arise from the femur and, with or without the intervention of the patella, insert on the *Caput tibiae.* Three such muscles generally occur in birds and all are more or less clearly defined in the crow and raven. In these two birds the outer subdivisions are very intimately grown together, and are inseparable throughout most of their extent. Shufeldt (1890, p. 169) called these two fused muscles the *extensor femoris;* the outer he called the *vastus externus* and the inner the *cruraeus.* The third or medial head of the Fem. tib. he considered

separately as the *vastus internus*. In the following account the terminology of Gadow for the three parts of this muscle will be used.

I. *M. femori-tibialis externus* (Fem. tib. ext.)

This is the *vastus externus* of Shufeldt. It arises fleshy from a large area on the outer and anterior aspect of the femur, all the way from the trochanter to the external condyle (Figs. 2, 8, 18-22). Distally its fibers contribute to the formation of the patellar tendon.

II. *M. femori-tibialis medius* (Fem. tib. med.).

This is the *cruraeus* of Shufeldt. It arises from the anterior aspect of the femur (Figs. 2, 11, 18-22), and on its external side is completely fused with the more laterally situated Fem. tib. ext. For this reason the two muscles have been labeled together in the figures as Fem. tib. ext. + med. Proximally the heads of these two muscles are quite narrow and are separated by the insertions of the Il. troc. ant. and the Il. troc. med. The insertions are less clearly separated, both contributing to the formation of the patellar tendon, which runs over the anterior border of the knee and inserts on the anterior crest of the tibial head; however, the bulk of the fibers of the larger Fem. tib. med. insert fleshy on the entire proximal end of the patella. (Fig. 7).

These two combined muscles are concealed laterally by the Il. tib., and medio-distally by the sartorius.

III. *M. femori-tibialis internus* (Fem. tib. int.)

This is the *vastus internus* of Shufeldt (1890, p. 172). It originates fleshy from a long, narrow and slightly oblique line on the medial side of the femoral shaft (Figs. 6, 18-22). This attachment extends in the crow from a point slightly beyond the insertion of the *M. iliacus* to the internal condyle (Fig. 9). In the raven it reaches up a little above the iliacus. Distally the muscle gives off a short strong tendon which inserts on the middle of the interno-proximal side of the head of the tibia, adjacent to the origin of the internal head of the *M. gastrocnemius* (Fig. 9). This muscle occurs superficially on the inner aspect of the thigh. Near the distal end it shows a rather definite indication of a division into a medial and a lateral portion.

Action.—The Fem. tib. ext. + med. make up the great extensor of the shank, although they are aided in this respect by the Il. tib. The Fem. tib. int. appears to rotate the head of the tibia inward.

Homology.—According to Gadow (1891, p. 157) the entire *M. femori-tibialis* corresponds for the largest part to the *extensor cruris quadriceps* of mammals, but also contains the *cruralis*, both *vasti*, and perhaps also a part of the *rectus femoris*. Inasmuch as this is not a clear-cut case of homology, it appears advisable to use the terminology of Gadow instead of trying to adopt BNA names for these muscles.

Comparison.—The Fem. tib. ext. is independently developed in the following forms: *Ardea, Grus, Fulica, Totanus* (Fig. 49), *Larus*, and *Zenaidura*. It arises from the posterior and lateral surfaces of the distal half (three-fourths in *Fulica)* of the femoral shaft and inserts on the lateral side of the anterior tibial crest. Superficially it is almost completely covered by the Fem

tib. med. and Il. tib. Gadow (1891, p. 155) states that in sea-gulls the outer and middle portions of the femori-tibialis are grown together. They are quite distinct in *Larus pipixcan*.

In *Gavia, Fregata, Pedioecetes, Colinus,* and *Corvus* the Fem tib. ext. reaches so far proximally as to separate the insertion of the Il. troc. ant. from that of the Isch. fem.

The femori-tibialis internus shows a very definite longitudinal division into two parts in *Buteo* (Fig. 67). Many other forms show a slight division as in *Corvus*.

In the following the Fem. tib. int. reaches proximally as far as or above the insertion of the iliacus: *Gavia, Colymbus, Sula, Chen, Cathartes, Buteo, Grus, Fulica, Totanus, Larus, Uria, Zenaidura, Chordeiles, Chaetura, Colaptes, Dryobates, Corvus corax sinuatus*. Gadow (1891, p. 156) says that in *Grus* the origin is limited to the distal half of the femur. This is wrong as far as *Grus canadensis* is concerned.

In *Fregata, Falco,* and *Coccyzus* the internal part is unusually short, especially in the first two, where it is limited to about the distal two-thirds of the femur. *Fregata* is peculiar in having the tendon of insertion bifurcated, one branch connecting with the patellar tendon, the other with the tibia.

The Fem. tib. ext. and med. insert fleshy together on the entire posterior surface of the long procnemial spine of the tibia in *Gavia*. In *Colymbus* they insert on the proximal surface of the long patella and on the medial side of the tibial spine.

M. PIRIFORMIS (Pirif.)

Femoro-caudal—Shufeldt (1890, p. 183).
M. caud-ilio-femoralis—Gadow (1891, p. 158).

Description (for the crow and raven).—Only the *Pars caudi-femoralis* is represented in the present subjects. It is a long, compressed and spindle-shaped muscle, passing from the base of the coccyx to the lateral side of the femur (Figs. 3, 8). From its origin on the latero-ventral aspect of the ventral apex of the coccyx, the piriformis sends forward a slender tendon which is covered laterally by the abdominal muscles. This tendon quickly changes over into a fleshy belly, which enters the musculature of the thigh between the semitendinosus and semimembranosus (Fig. 19), and passes on forward (covered laterally by the Bic. fem.) to the postero-outer side of the end of the proximal third of the femoral shaft, where it changes into a short, compressed tendon (Fig. 3). Shortly before the insertion it is crossed externally by the large ischiadic nerve and artery, and farther forward and medially by the femoral vein.

There is a difference of opinion as to which end of the muscle constitutes the origin. Burt (1930, p. 502) considers the femoral attachment as the origin. Gadow based his interpretation of this question on the fact that the caudal attachment is on the vertebral column.

Action.—Both ends of the muscle are attached to movable bones; hence,

by its contraction the femur tends to move backward and the tail laterally and downward.

Homology.—According to Gadow (1891, p. 162) the *M. caud-ilio-femoralis* corresponds to the *M. pyriformis (piriformis* of the BNA*)* of mammals.

Comparison.—This double muscle was used by Garrod in his myological formula. The *Pars caudi-femoralis* is indicated by the letter "A" and the *Pars ilio-femoralis* by "B." One or the other or both are present in all forms examined.

Both present (AB)	P. il. fem. absent (A present)	
Gavia	*Fregata*	*Otus*
Chen	*Sula*	*Coccyzus*
Pedioecetes	*Ardea*	*Chordeiles*
Colinus	*Catharies*	*Chaetura*
Grus	*Buteo*	*Colaptes*
Fulica	*Falco*	*Dryobates*
Uria	*Totanus*	*Tyrannus*
Zenaidura	*Larus*	*Corvus*
	Bubo	

The P. caud. fem. was found to be absent in *Colymbus* only.

In most forms the P. caud. fem. arises by a tendon very much as in *Corvus*, but in *Colinus* (Fig. 64) and *Zenaidura* the origin is rather thick and fleshy. In all species studied the P. caud. fem. arises only from the ventral surface of the coccyx. Gadow (1891, p. 159) is therefore wrong when he gives the origin as coming from the transverse processes of several caudal vertebrae in Carinates.

In *Grus* the two parts are independent throughout, but in most forms possessing both they unite shortly before inserting on the femur. The P. caud. fem. usually inserts about one-third the way down the femur; however, in *Fregata, Chen, Buteo, Uria,* and *Chaetura* the attachment is about midway the femur. In *Chen* it extends well below the middle. On the other hand the insertion is far up on the femur in *Pedioecetes,* being opposite the insertion of the Il. troc. ant. *Fregata, Sula,* and *Chaetura* have this tendon of insertion very long and slender.

The P. il. fem. (Fig. 64) usually arises from the postero-lateral side of the ilium and ischium. In *Uria* the origin is only from the ischium; from the ilium only in *Colymbus, Grus,* and *Zenaidura,* the origin in the first two being from about the middle of the lateral ridge of the post-acetabular ilium.

The piriformis is very weakly developed in *Fregata, Ardea, Grus, Larus, Bubo,* and *Otus.*

M. SEMITENDINOSUS (Semit.)

Semitendinosus—Shufeldt (1890, p. 177)
M. caud-ilio-flexorius—Gadow (1891, p. 162).

Description (for the crow and raven).—This muscle arises partly fleshy from about the posterior fifth of the post-acetabular ridge of the ilium (Figs. 1, 2, 8, 18-22); and, posterior to this it continues as a thin fascia which connects with the transverse processes of several proximal caudal vertebrae. This aponeurotic fascia separates the intrinsic muscles of the tail into a dorsal and

a ventral group, and, besides the caudal attachment, it also connects with the posterior border of the ilium. This fascia has not been shown in the figures because its exact extent is very difficult to determine, especially posteriorly where it blends with the musculature of the tail and abdominal wall.

From its origin the band-shaped belly passes downward along the posterolateral margin of the thigh to the posterior side of the knee region, where it is divided by a fibrous ligament. Beyond this ligament the fleshy belly continues forward as the *accessorius semitendinosi*, to insert on the posterior side of the femur just above the condyles (Fig. 14). The ligament which divides the muscle into two parts passes downward from the posterior angle of the muscle to insert on the proximal part of the *M. gastrocnemius*, especially on the *Pars media*. Besides this it makes a strong connection with the tendon of the semimembranosus.

Shufeldt (1890, p. 179) discussed the accessory semitendinosus as a separate muscle, and described it as arising from the femur and inserting on the tendinous raphe between this muscle and the semitendinosus proper. Burt (1930, p. 502) followed Shufeldt in this. Gadow (1891, p. 163) gives a rather extended discussion of why the so-called "accessorius" should be considered as a femoral insertion of the semitendinosus, and not as a second head of origin.

Action.—Pulls the femur posteriorly, at the same time flexing the shank somewhat.

Homology.—Gadow (1891, p. 166) states that the *M. caud-ilio-flexorius* corresponds to the *M. semitendinosus* of mammals.

Comparison.—This usually double muscle is also included in Garrod's myological formula. The semitendinosus proper is designated as "X" and the accessorius as "Y."

Both Parts present		Accessorius absent	Both absent
Ardea	*Totanus*	*Gavia*	*Fregata*
Butorides	*Larus*	*Colymbus*	*Buteo*
Cathartes	*Coccyzus*	*Sula*	*Falco*
Pedioecetes	*Chordeiles*	*Chen*	*Chaetura*
Colinus	*Colaptes*	*Uria*	*Bubo*
Grus	*Tyrannus*	*Dryobates*	*Otus*
Fulica	*Corvus*		
Zenaidura			

In most cases the semitendinosus arises from the posterior edge of the ilium and also from the proximal caudal vertebrae; however, in *Gavia, Colymbus, Grus,* and *Fulica* there is no connection with the vertebrae. In *Gavia, Sula,* and *Uria,* the pelvic attachment extends downward onto the ischium. The origin is mainly from the ischium in *Cathartes.*

Shortly before its insertion this muscle is commonly connected with the P. med M. gas., but in the following no such connection exists: *Gavia, Colymbus, Sula, Uria, Chen,* and *Dryobates.*

Ordinarily the tendon of insertion of the semitendinosus is intimately connected with that of the semimembranosus. In *Colymbus* and *Dryobates* this muscle is independent throughout its course. In *Chen* on the other

hand the two insert by a single common tendon. The tendon of insertion is usually wide but in *Gavia* it is very long and slender. *Colymbus* is somewhat similar.

In *Larus* Gadow (1891, p. 163) considers that the accessorius forms a direct continuation of the P. med M. gas., thus making it appear that the semitendinosus inserts directly on the middle head of the gastrocnemius. However, in *Larus pipixcan* this is not the case for the middle head of the gastrocnemius is plainly discernible and has no unusual connection with the accessorius.

M. SEMIMEMBRANOSUS (Semim.)

Semimembranosus—Shufeldt (1890, p. 180)
M. ischio-flexorius—Gadow (1891, p. 166)

Description (for the crow and raven).—This band-shaped muscle makes up the postero-inner border of the thigh musculature (Figs. 3, 6, 18-22). It arises fleshy from the posterior edge of the ischium (Fig. 8), and also to a slight extent from the abdominal muscles posterior to this. From this point it passes downward to the posterior side of the knee region, where it enters the musculature of the shank between the inner and middle heads of the *M. gastrocnemius,* and inserts by a wide but very thin tendon on the inner side of the tibial shaft (Fig. 9). Just proximal to the insertion there is a rather intimate fibrous connection with the tendon of the semitendinosus.

Action.—Flexion of the shank.

Homology.—According to Gadow (1891, p. 168) the *M. ischio-flexorius* of birds corresponds to the M. semimembranosus of mammals.

Comparison.—This is one of the most uniform of the thigh muscles and is present in all except *Colymbus*. In most cases the origin is from the postero-lateral surface of the ischium and the adjacent pubis; confined to the ischium in *Ardea, Fulica, Larus, Colaptes, Tyrannus,* and *Corvus*. It is located far forward in *Gavia* and *Chen,* being from the mid-ventral part of the ischium. In the former it extends forward almost to the posterior edge of the ischiadic foramen.

Usually the tendon of insertion is more or less intimately connected with that of the semitendinosus. In *Chen* the two insert by a common tendon. In *Colaptes* and *Dryobates* the insertions are not opposite as is ordinarily the case but the Semim. inserts distally to the Semit. In *Grus, Fulica, Pedioecetes,* and *Colinus* the Semim. is connected by heavy fascia to the accessorius and also to the middle and inner heads of the gastrocnemius.

The muscle is weakly developed in *Sula* and *Colinus*.

Falco shows a peculiar development of this muscle. It is made up of two distinct parts which originate and insert together (Figs. 46, 65).

In the specimen of *Colymbus* available no trace could be found of the Semim. Gadow (1891, p. 167) states that this muscle is probably present in all birds although at times very much reduced as in *Podiceps,* etc. Garrod (1873, p. 629) states that it may sometimes be absent in grebes as claimed by Sundevall.

M. BICEPS FEMORIS (Bic. fem.)

Biceps flexor cruris—Shufeldt (1890, p. 174).
M. ilio-fibularis—Gadow (1891, p. 168).

Description (for the crow and raven).—This large triangular muscle arises from a long narrow line on the dorso-lateral ridge of the hinder part of the ilium, just below the line of origin of the Il. tib. (Figs. 1, 2, 8). The anterior part of this origin is by a thin aponeurotic tendon which overlaps the posterior part of the Il. troc. post. The posterior part of the origin of the Bic. fem. is quite fleshy and is attached to a much wider line on the ilium. From its origin the muscle passes downward as a wide but rather thin fleshy sheet (Figs. 18-22). Its fibers converge toward the posterior side of the knee region, where the muscle passes through a tendinous loop in company with one of the main branches of the ischiadic nerve. Insertion is by a strong tendon on a slight tubercle on the postero-outer side of the shaft of the fibula, about midway the point where this bone is fused with the tibia (Figs. 8, 23).

The above mentioned tendinous loop is connected with the outer aspect of the external condyle of the femur by both of its principal arms, which are directed forward and upward (Fig. 3). The more distal of these is closely fused on its outer side with the tendon of origin of the external head of the *M. gastrocnemius*. In addition to these two there is a third arm to the loop. This connects the posterior part of the more distal femoral arm with the strong tendon which gives origin to the external head of the F. hal. l. and to several of the perforated flexors. This third arm is covered laterally by the belly of the F. p. et p. d. II. Shufeldt (1890) does not mention this third arm to the biceps loop; however, it is well developed in the raven.

Laterally the Bic. fem. is covered only in part by the hinder portion of the Il. tib.

Action.—This muscle is the powerful flexor of the shank.

Homology.—Gadow (1891, p. 170) states that the *M. ilio-fibularis* represents the *M. biceps cruris* of mammals, and perhaps also a portion of the *M. gluteus maximus*. According to the BNA, *M. biceps femoris* is the name that should be applied to this muscle.

Comparison.—The biceps is one of the most uniform muscles and is present in all forms examined. The slight variations are mainly concerned with the origin which usually extends tendinous in front of the femur very much as in the crow. In the following it is restricted to the acetabular and post-acetabular ilium: *Gavia, Colymbus, Chen, Buteo, Falco, Coccyzus, Bubo, Otus, Colaptes,* and *Dryobates*.

As a rule the biceps is more or less concealed superficially by the posterior portion of the Il. tib. In the following, however, it is entirely visible superficially: *Fregata, Buteo, Falco, Chaetura, Bubo, Otus,* Tyrannidae, and Hirundinidae. In such cases the proximal portion of the muscle is usually fused anteriorly with the posterior margin of the Il. tib.

The origin in *Colymbus* is from the middle region of the post-acetabular ridge of the ilium, and the muscle is completely concealed by the Il. tib.

In *Chen* the origin is from about the anterior half of the post-acetabular ilium.

In every case the biceps loop consists of the three tendinous arms very much as in the crow. The two femoral arms are very long in *Gavia* and *Colymbus* since the biceps inserts just a little above the middle of the shank.

M. ISCHIO-FEMORALIS (Isch. fem.)

Obturator externus—Shufeldt (1890, p. 186).
M. ischio-femoralis—Gadow (1891, p. 170).

Description (for the crow and raven).—This muscle is quite short and bulky (Figs. 3, 18). It originates fleshy from the greater part of the lateral surface of the ischium lying between the ischiadic foramen, the *Foramen oblongum* (Gadow, 1891, p. 78), and the lateral iliac ridge (Fig. 8). At the posterior rim of the ischiadic foramen this muscle also overlaps a little into the inside of the pelvis (Figs. 6, 9). From the point of origin it extends forward to the outer side of the trochanter, where the fibers converge into a short flat tendon before inserting just behind the proximal end of the Fem. tib. ext. Laterally the Isch. fem. is covered largely by the Bic. fem. and the piriformis. Shortly before its insertion on the femur the muscle is crossed externally by the large ischiadic nerve and artery.

Action.—Draws the femur backward, at the same time rotating it in this direction.

Homology.—Gadow (1891, p. 171) states that the *M. ischio-femoralis* seems to correspond to the *M. quadratus femoris* and perhaps also to the *gemelli* of mammals. Because of this uncertainty it seems advisable to retain the name used by Gadow instead of trying to apply a BNA name of doubtful homology.

Comparison.—The Isch fem. is extremely uniform throughout the series of birds examined, showing practically no modifications worth mentioning. In *Corvus* and many others the origin extends to the hinder margin of the ischium but in *Gavia, Chen,* and *Pedioecetes* it is limited to about the anterior half.

M. OBTURATOR INTERNUS (Obt. int.)

Obturator internus—Shufeldt (1890, p. 190).
M. obturator—Gadow (1891, p. 171).

Description (for the crow and raven).—This is a flat triangular muscle which lies on the inside of the pelvis (Fig. 6), separated from the viscera only by the peritoneal membrane. Anteriorly its fibers converge into a strong tendon which passes to the outside through the obturator foramen. This muscle arises from a large area on the medial surface of the ischium, and also from the dorsal half of the medial surface of the pubis bounding the *Foramen oblongum* (Fig. 9). I have been unable to demonstrate that this muscle also arises from the Ischio-pubic membrane as claimed by Shufeldt (1890, p. 191).

After passing through the obturator foramen the tendon goes to the postero-outer side of the trochanter, where it inserts in common with the *M. obturator externus* (Figs. 4, 14). The latter muscle is strongly attached

by fleshy fibers to the medial surface of the tendon of the Obt. int. Laterally the tendon of this muscle is largely covered by that of the Isch. fem.

Action.—The two obturator muscles work together in rotating the femur backward and inward.

Homology.—According to Gadow (1891, p. 173) the *M. obturator* of birds corresponds to the *M. obturator internus* of mammals. The latter name should, of course, be used.

Comparison.—The Obt. int. is present in all species studied and is subject to comparatively little modification in the various groups of birds. Usually the belly is broad and more or less rounded as in the crow, but in the following it is long and slender: *Gavia, Colymbus, Fregata, Sula, Larus, Totanus, Uria, Zenaidura, Chordeiles, Chaetura.* In these the origin is limited mainly to the edges of the *Foramen oblongum.*

In *Fulica, Porzana carolina,* and *Colinus* the muscle is very peculiar in having at the anterior edge of the belly a lateral extension which arises from the ventral surface of the latero-posterior portion of the ilium. This part of the Obt. int. is visible externally through the *F. isch.*, passing across the posterior half of this opening. *Fulica* and *Porzana* differ from *Colinus* in having the smaller anterior part which arises from the ilium differentiated as a more or less separate muscle. The two parts form separate tendons which pass together through the obturator foramen, uniting incompletely before inserting on the femur.

In many forms the carneous portion of the muscle passes out through the obturator foramen along with the tendon, continuing in some cases quite to the insertion. This is especially evident in *Sula, Colinus, Grus, Totanus,* and *Coccyzus.*

As a rule the tendon of insertion is more or less closely connected with the Obt. ext. but in *Totanus* the two are independent.

M. OBTURATOR EXTERNUS (Obt. ext.)

Gemellus—Shufeldt (1890, p. 194).
Mm. accessorii M. obturatoris—Gadow (1891, p. 173).

Description (for the crow and raven).—This small muscle is fleshy throughout and arises by two distinct heads (Fig. 4). The smaller of these originates from a small area on about the middle of the ventral border of the ischiadic foramen. The larger head originates more anteriorly from the point of fusion of the ischium and pubis which lies between the acetabulum and the ischiadic and obturator foramina (Fig. 8). The fibers of these two heads unite before inserting on the posterior side of the trochanter, just medial to the insertion of the Obt. int. (Fig. 14). In addition numerous fibers insert on the medial side of the tendon of the latter muscle. The Obt. ext. is brought into view upon the removal of the Isch. fem., although it is then still partly covered by the tendon of the Obt. int.

Action.—Aids the Obt. int. in rotating the femur backward and inward.

Homology.—According to Gadow (1891, p. 174) the *Mm. accessorii M. obturatoris* is comparable to the *M. obturator externus* of mammals.

Comparison.—The Obt. ext. is present in all birds studied. Usually it consists of a single belly but in some there are two separate parts; however, this is rather difficult to determine satisfactorily without an abundance of duplicate specimens since this short deeply-buried muscle is hard to expose without removing all the other muscles of this region.

It consists of two quite distinct parts in *Grus, Fulica, Larus, Uria, Tyrannus,* and *Corvus.* In *Tyrannus* and *Corvus* the smaller posterior head arises from about the middle of the ventral border of the F. isch. In the others this arises from the edges of the F. obt. and inserts mainly on the tendon of the Obt. int. Gadow (1891, p. 174) indicates that this muscle is undivided in Passeres.

M. ADDUCTOR LONGUS ET BREVIS (Add. long.)

Adductor longus and *Adductor magnus*—Shufeldt (1890, pp. 194-199).
M. pub.-ischio-femoralis—Gadow (1891, p. 174).

Description (for the crow and raven).—This is a large muscle and is the most medial of all the thigh muscles lying posterior to the femur (Figs. 4, 6, 18-22). It is divided lengthwise into two very distinct parts which will be discussed separately.

Pars anterior.—Arises from a narrow line extending from the posterior margin of the obturator foramen, backward on the ischium along the antero-dorsal border of the *Foramen oblongum* (Fig. 8). From here the wide flat belly extends downward and forward to the postero-inner side of the femoral shaft where it inserts on a large area (Fig. 14). This insertion is bounded laterally by the Fem. tib. ext., medially by the Fem. tib int., and distally by the insertion of the *accessorius semitendinosi.* The *Pars anterior* is fleshy almost throughout. This is the *Adductor longus* of Shufeldt.

Pars posterior.—Arises partly tendinous from a narrow line on the lateral surface of the ischium, directly behind the origin of the *Pars anterior.* This attachment extends along the dorsal border of the *Foramen oblongum* to a point about opposite the posterior end of the Isch. fem. (Fig. 8). The strong belly extends forward and downward parallel to the *Pars anterior.* At the postero-inner side of the knee region the muscle gradually converges toward its insertion on the postero-inner surface of the proximal end of the internal condyle of the femur (Fig. 9). This is the *Adductor magnus* of Shufeldt.

The two parts of the *M. adductor longus et brevis,* although easily separable, are quite intimately connected at their point of contact.

Action.—A powerful flexor of the thigh.

Homology.—Gadow (1891, p. 176) states that the *M. pub.-ischio-femoralis* is to be compared with the *M. adductor longus* and perhaps also with the *adductor brevis* of mammals.

Comparison.—This muscle is present in all forms examined. Typically it consists of two layers, a *Pars interna* and a *Pars externa* (Figs. 46-49). The

entire muscle may be fleshy, or either one or both parts may be tendinous at the origin. In addition the P. int. may have a tendinous insertion but that of the P. ext. is always fleshy. These two parts are more or less completely fused and the muscle appears to be a single layer in *Gavia, Larus, Uria, Zenaidura, Chaetura, Colaptes,* and *Dryobates*. The muscle is almost completely fleshy in *Gavia, Fregata, Sula, Grus,* and *Uria*. The P. int. inserts mainly as a thin aponeurotic sheet in *Colymbus, Chen, Cathartes, Buteo, Falco,* and *Fulica*. In most cases the P. ext. is the larger of the two but in *Fregata* and *Pedioecetes* it is much smaller, being rather narrow and only about one-fifth the bulk of the inner part.

The origin is usually from the ventral edge of the ischium and the adjacent pubis, that of the P. ext. being just above that of the P. int. In *Coccyzus* and *Chordeiles* the muscle is rather weakly developed and the origin is limited to about the front half of the ischium. The origin in *Chaetura* is from the ventral edge of the pubis only.

The insertion is usually on a long line down the posterior surface of the femur. In *Uria* it extends along the posterior side of almost the entire femoral shaft. *Gavia* is very peculiar in having the insertion by a rather narrow tendon on the medial surface of the internal condyle only.

In almost all forms the distal end of the P. int. is more or less firmly fused with the P. med. M. gas. However, in *Coccyzus* and *Chordeiles* there is little or no connection between the two.

It is difficult to homologize between the P. post. and the P. ant. of this muscle in *Tyrannus* and *Corvus* and the inner and outer portions in other forms. Since the P. post. in these two genera connects distally with the P. med M. gas., it is probable that it represents the P. int.

M. TIBIALIS ANTERIOR (Tib. ant.)

Tibialis anticus—Shufeldt (1890, p. 211).
M. tibialis anticus—Gadow (1891, p. 177).

Description (for the crow and raven).—This powerful muscle lies on the anterior border of the shank and is largely covered by the more superficial Per. long. (Figs. 1, 2, 7). It originates by two distinct heads, the anterior of which arises fleshy from a rather narrow line on the anterior side of the tibial crest, adjacent to the proximal end of the Ext. dig. 1. (Figs. 11, 12). The attachment to the antero-external side of the tibial crest is much more extensive than that to the inner side (Figs. 8, 9). The posterior or femoral head is much smaller than the foregoing, and arises from the distal apex of the external condyle as a strong tendon which passes distally between the head of the fibula and the lateral apex of the tibial crest. It soon becomes fleshy and fuses somewhat above the middle of the tibio-tarsus with the tibial head (Figs. 2, 23-32). From here the muscle gradually narrows, as it proceeds downward, into a strong tendon which just above the malleoli passes under a fibrous loop in company with the Ext. dig. 1. This loop holds the muscles firmly in place. Below the loop the tendon passes between the malleoli, and widens out and again contracts before inserting on a tubercle

on the antero-internal aspect of the tarso-metatarsus, near the proximal end of that bone (Fig. 10).

Action.—A powerful flexor of the tarso-metatarsus upon the shank.

Homology.—This muscle corresponds to the *M. tibialis anticus* of mammals and reptiles Gadow (1891, p. 178). The BNA name for this is *M. tibialis anterior.*

Comparison.—This very uniform muscle is present in all forms. Usually the femoral head is much the smaller but in *Uria* the two parts are about equal in size. In *Gavia* the femoral portion is very short, uniting far up with the main head. In *Buteo* and *Falco* the origin of the tibial head is unusually extensive, coming from the anterior tibial crest and also from a long line down the medial surface of the shaft of the tibia.

In addition to the usual insertion there is given off in many forms a small but definite branch from the main tendon, which runs farther distad to insert in various ways. Such an extra tendon is found in *Gavia, Colymbus, Fregata, Chen, Ardea, Buteo, Falco, Fulica, Totanus, Coccyzus,* and *Chordeiles.* It was not found in the other forms studied. *Falco* even shows a still smaller third tendon (Fig. 54). In most cases the small branch comes off of the main tendon just below the intertarsal joint and passes distad, widening out and inserting on the sides of the tarso-metatarsus, thus holding the tendon of the Ext. dig. l. in place very much as the tendon of the gastrocnemius ensheaths the flexor tendons on the posterior side of the tarsus.

In *Fregata* the tendon of insertion gives off a strong lateral branch which, instead of becoming attached to the tarso-metatarsus, forms the head of origin of one part of the Ext. brev. d. IV.

The insertion in *Bubo* and *Otus* is in the usual place but is by two distinct tendons, one anterior and the other posterior (Figs. 55, 63). These tendons seem to correspond to the anterior and posterior heads of origin, for the posterior tendon is smaller just as the femoral head of origin is smaller. This makes the whole muscle appear double, the two parts being fused only in the middle.

M. EXTENSOR DIGITORUM LONGUS (Ext. dig. l.)

Extensor longus digitorum—Shufeldt (1890, p. 215).
M. extensor digitorum communis—Gadow (1891, p. 178).

Description (for the crow and raven).—Arises fleshy from an extensive area on the antero-inner side of the proximal half of the tibio-tarsus (Fig. 12). I am unable to find a small second head of origin as described by Shufeldt (1890, p. 217). The slender pennate belly is divided lengthwise throughout its lower extent by a tendinous band which is continuous below with the tendon (Figs. 4, 6, 23-37). As the muscle proceeds downward from its origin it becomes gradually narrowed upon merging with the tendon, which is directed obliquely outward toward the center of the bone, and passes through the fibrous loop shortly above the malleoli in company with the Tib. ant. Just below this fibrous loop the Ext. dig. l. passes alone beneath a bony bridge which holds the tendon firmly against the tibio-tarsus. Below this bony bridge the tendon is directed along the antero-medial border of the tarso-metatarsus by a

second bony bridge on the antero-inner side of that bone, near its proximal end (Fig. 10). From here the tendon passes, medial to the insertion of the Tib. ant., down the anterior side of the tarso-metatarsus, and just above the base of the fore toes divides into three tendons, one of which goes to each of the last three digits (Fig. 4). The insertions of these various branches are rather complex; hence they will be described separately.

Index digit. The branch to the index digit passes down the anterior border of this toe, and about midway the proximal phalanx sends off a small outer branch which inserts upon the antero-outer border of the proximal end of the second phalanx. The inner branch becomes gradually broader as it proceeds distally to its insertion on the base of the unguinal phalanx (Figs. 4, 10, 39, 40).

Medius digit. This branch is the largest and lies directly between the other two. A little beyond the middle of the proximal phalanx the tendon bifurcates. The inner of these branches divides immediately into a short outer branch which encloses a small sesamoid and inserts on the proximal end of the second phalanx, and a slender inner branch which passes down the antero-medial border of the toe, and about midway the second phalanx becomes fused laterally with the main median branch. A little beyond this it again becomes free and shortly before reaching the base of the bony claw unites in the antero-median line with the main outer branch.

Shortly beyond the base of the second phalanx the initial lateral branch divides into a median branch and an outer branch. This large median branch inserts on the base of the third phalanx.

The outer tendon sends off a short medial branch which inserts on the base of the third phalanx in common with the main median branch. This outer branch then continues distad to unite in the antero-median line with the most medial branch of all, as mentioned above. These two united branches then insert together on the base of the bony claw (Figs. 4, 10, 41, 42).

Quadratus digit. At a point about opposite the middle of the second phalanx the tendon to the fourth toe divides into two branches. The inner of these soon divides into a short outer branch which inserts usually on the base of the third phalanx (but frequently on the distal end of the second phalanx), and a more slender inner one which inserts on the base of the fourth phalanx.

The outer main branch proceeds distad and becomes gradually broader toward its insertion on the base of the unguinal phalanx (Figs. 4, 10, 43-45).

From this it will be seen that the Ext. dig. l. makes eight distinct points of attachment on the bases of the distal phalanges of the fore toes: two on the index, three on the medius, and three on the quadratus. The exact attachments of these tendons are subject to considerable variation in different individuals, but the discriptions given above probably represent about the average condition.

In its upper fleshy portion the Ext. dig. l. is covered medially by the internal head of the gastrocnemius, and anteriorly and laterally by the Tib. ant.

Action.—This muscle is the great extensor of the fore toes. At the same time it tends to flex the tarso-metatarsus upon the shank.

Homology.—Gadow (1891, p. 180) states that this muscle corresponds to the *M. extensor digitorum pedis longus* of mammals and reptiles. According to the BNA it should be called the *M. extensor digitorum longus.*

Comparison.—Present in all forms and subject to little modification except at the distal end. The origin is usually from the anterior surface of about the proximal half of the tibia, but in *Gavia* it extends about three-fourths the way down this bone. In *Bubo* and *Otus* this muscle arises in addition from the anterior surface of the fibula, from the *Caput fibulae* to about midway the shank.

The loop or bridge under which the tendon passes just above the malleoli is bony in all except *Bubo* and *Otus,* in which it is fibrous. The second loop on the anterior side of the proximal end of the tarso-metatarsus is fibrous in all except the following in which it is bony: *Fulica, Zenaidura, Chaetura, Bubo, Otus, Colaptes, Dryobates, Tyrannus,* and *Corvus.*

In most forms as in the crow the main tendon divides just above the base of the fore toes, sending branches to each of the last three digits. In *Pediocetes, Colinus, Bubo,* and *Otus* the tendon divides much higher up, nearer the middle of the tarsus, into two branches. The inner branch passes to the index digit and the outer supplies the third and fourth. However, in *Pediocetes* and *Colinus* the inner tendon supplies the inner side of the medius and also the index digit, the outer branch serving the outer side of the medius and the fourth.

The exact mode of insertion on the fore toes is made in the most variable and confusing manner in the different bird groups. Nevertheless a few conspicuous modifications can be pointed out. The simplest condition is found in *Chaetura* in which the tendons insert on the unguinal phalanges only. In *Colaptes* and *Dryobates* there is only one tendon to each toe. That to the index inserts only on the unguinal phalanx. The branch to the third toe sends off short side branches to the various phalanges, but the principal insertion is on the bony claw. The tendon to the fourth toe inserts only on the bony claw. *Bubo* and *Otus* agree with these woodpeckers in having only one main branch to each toe, but differ slightly in the exact method of insertion.

In some birds there is only one tendon passing along the lateral side of the penultimate phalanx of the third digit. In others there are two, one on either side. The following is a synopsis of the forms that show clearly one condition or the other:

One tendon	Two tendons
Sula	*Gavia*
Ardea	*Fregata*
Pediocetes	*Cathartes*
Colinus	*Fulica*
Uria	*Zenaidura*
Chordeiles	*Coccyzus*
	Tyrannus
	Corvus

In many the tendons of insertion are rather diffuse and vaguely defined, especially on certain digits. This is true of *Colymbus, Grus, Larus,* and *Totanus.*

M. PERONAEUS LONGUS (Per. long.)

Peroneus longus—Shufeldt (1890, p. 208).
M. peroneus superficialis—Gadow (1891, p. 180).

Description (for the crow and raven).—Arises partly tendinous from the antero-proximal border of the anterior tibial crest (Fig. 12), and to a slight extent from the fascia covering the knee joint. This is the most superficial muscle on the antero-external side of the shank, and its thin semitendinous belly is rather intimately attached to the underlying muscles. About two-thirds of the way down the shank the muscle tapers rather suddenly to form the strong tendon which runs obliquely backward and downward on the lateral side of the bone. Just above the malleoli the tendon sends off on the posterior side a short branch which becomes attached to the lateral edge of the proximal end of the so-called "tibial cartilage" Shufeldt (1890, p. 210). The main tendon continues downward over the external malleolus and the lateral side of the base of the tarso-metatarsus, to the posterior side of the latter bone (Figs. 1, 6, 23-33). Shortly below the perforated process it unites with the tendon of the Flex. per. d. III (Fig. 4).

In connection with the proximal insertion of this muscle, Gadow (1891, p. 181) considers that the tibial cartilage is a part of the shorter tendon of the Per. long., and that since this is perforated by several of the toe flexors it forms a sustentaculum for them. He gives no basis for this interpretation, and if his view is correct, this muscle then presents a very curious and unusual condition in which one of the tendons of insertion becomes enormously enlarged (the tibial cartilage), and is perforated by seven flexor tendons. This can hardly be the case since in owls the Per. long. is absent but the tibial cartilage is well developed. This fibro-cartilaginous mass glides over the end of the tibio-tarsus in the posterior sulcus which lies between the malleoli. It becomes attached to the proximal end of the perforated process.

Action.—The Per. long. helps to extend the tarso-metatarsus and, because of its connection with the Flex. per. dig. III, also aids in flexing the third toe.

Homology.—Gadow (1891, p. 182) states that this muscle is homologous to the *M. peroneus* (*peronaeus* of the BNA) *longus* of mammals.

Comparison.—Present in all except *Chaetura, Bubo,* and *Otus.* The origin is extremely variable among the different groups but in the majority it is from the anterior tibial crest as in the crow. In addition it is closely attached to the underlying muscles. In the following the origin is tendinous from the lateral edge of the tibial crest and fleshy from the shaft of the fibula: *Colymbus, Fregata, Sula, Buteo, Larus, Uria, Zenaidura,* and *Coccyzus.* The origin is also partly from the shaft of the tibia in *Larus* and *Coccyzus.* In these forms the muscle is usually very narrow and consequently does not cover any considerable portion of the Tib. ant. The origin in *Falco* is restricted

to the fibula and the adjacent muscles. In *Gavia* it is from the underlying muscles only.

The typical insertion is bifurcated as in the crow, one branch going to the tibial cartilage and the other to the tendon of the Flex. per. d. III. However, in the following the muscle has no connection with this perforated flexor tendon: *Gavia, Colymbus, Colaptes, Dryobates, Melanerpes erythrocephalus,* and *Sphyrapicus varius.* In *Gavia* the tendon bifurcates as usual but the longer branch dwindles out on the fascia of the heel joint. In the others there is no bifurcation but the insertion is entirely on the tibial cartilage. Gadow (1891, p. 181) gives this type of insertion only for *Podiceps.* Burt 1930, p. 504) describes it for *Ceophloeus pileatus.*

In *Fregata* the tendon of insertion is reinforced just above the external malleolus by a branch from the Per. brev. The longer tendon joins that of the Flex. per. d. Ill very far down—just above the base of the toes.

M. PERONAEUS BREVIS (Per. brev.)

Tibialis posticus—Shufeldt (1890, p. 227).
M. peroneus profundus—Gadow (1891, p. 182).

Description (for the crow and raven).—This rather short but slender muscle lies along the postero-external border of the belly of the Tib. ant. (Figs. 1, 2, 3). It arises mostly fleshy from a long narrow line on the lateral side of the tibia and fibula, from about the insertion of the Bic. fem. to a point about two-thirds of the way down the tibio-tarsus (Fig. 8). Well above the malleoli the muscle changes into a strong tendon which passes over the lateral surface of the external malleolus to its insertion on the extreme latero-proximal end of the tarso-metatarsus (Figs. 23-29). Just above the external malleolus the tendon passes under a strong fibrous loop which holds it firmly in place.

Action.—Abduction of the tarso-metatarsus.

Homology.—According to Gadow (1891, p. 183) this muscle corresponds to the *M. peroneus* (*peronaeus* of the BNA) *brevis* of mammals.

Comparison.—The peronaeus brevis is present in all except *Colymbus, Sula,* and *Chordeiles.* Gadow (1891, p. 183) states that it is represented by a small tendinous cord in *Podiceps,* but I can find no trace of it in *Colymbus.* Gadow does not mention its absence in *Sula* but does indicate that it is absent in *Caprimulgus.* This authority further states that the Per. brev. is absent in *Ardea;* nevertheless it is well developed in *Ardea herodias.*

Typically the origin is fleshy from the lateral side of the fibula and tibia as already described for *Corvus.* In *Bubo* and *Otus* the distal end of the origin extends medially onto the anterior surface of the tibia, thus lying directly behind the Ext. dig. l. In *Gavia* the distal end of the origin extends backward onto the latero-posterior surface of the tibia.

The muscle is short and stout in *Fregata,* being limited to about the distal third of the tibial shaft. The origin is from the distal end of the fibula and the antero-outer edge of the tibia just above the external malleolus. The

proximal portion of the muscle gives off a tendon which unites with that of the Per. long. The main part inserts as usual.

The Per brev. is also rather short and stout in *Zenaidura*. The belly is very weak and slender in *Totanus, Larus,* and *Uria*.

In many birds the insertion is on the middle of the postero-proximal edge of the tarso-metatarsus. This is well illustrated by *Fulica* in which the tendon passes abruptly toward the inner side at the intertarsal joint in order to reach the point of attachment.

The insertion is on the latero-proximal edge of the tarso-metatarsus in the following: *Gavia, Fregata, Cathartes, Chen, Buteo, Falco, Zenaidura, Coccyzus, Bubo, Otus, Colaptes, Dryobates, Tyrannus,* and *Corvus*.

M. GASTROCNEMIUS (Gas.)

Gastrocnemius—Shufeldt (1890, p. 200).
M. gastrocnemius—Gadow (1891, p. 183).

Description (for the crow and raven).—This is the largest muscle of the pelvic appendage. It covers superficially a large surface of the anterior, inner and posterior borders of the shank, and arises by three distinct heads which will be described separately.

Pars externa.—Arises partly tendinous from the lateral surface of the external condyle of the femur, just in front of the femoral origin of the F. dig. l. and just distal to the anterior margin of the insertion of the *Accessorius semitendinosi* (Figs. 1, 8). It is closely connected with the distal arm of the tendinous loop for the Bic. fem. This head is intermediate in size between the other two, and passes down the postero-lateral border of the shank.

Pars media.—This, the smallest head, is very intimately connected with the semitendinosus by a heavy fibrous band, previously described. It arises partly fleshy from the posterior edge of the proximal end of the internal condyle of the femur, in common with the insertion of the posterior belly of the *M. adductor longus et brevis* (Figs. 6, 9). It passes downward on the inner side of the shank.

Pars interna.—This head about equals in bulk the other two combined. It arises mostly fleshy from a rather large area on the internal side of the head of the tibia (Fig. 9). From here it passes downward on the antero-internal border of the shank (Fig. 6). It is separated from the *Pars media* by the tendon of insertion of the semimembranosus.

At a point about one-third the way down the tibio-tarsus these three heads unite, and below this the combined muscle tapers gradually on the posterior border of the shank into a broad flat tendon which passes over the posterior side of the ankle joint (Figs. 23-34). It inserts on the posterior edge of the tarso-metatarsus—on the perforated process and on the lateral ridge (Fig. 13). This common tendon is the *Tendo Achillis,* and it seems to be continuous with a sheet of fascia which forms a thin sheath around the posterior side of the flexor tendons, holding them firmly into the posterior sulcus of the tarsus.

Gadow (1891, p. 185) even considers the connective tissue sheaths which hold the flexor tendons in place on the volar surfaces of the fore toes as being a distal continuation of the middle part of the *Tendo Achillis*.

Because of the great complexity of the insertion of this muscle only the main attachments are shown in the figures.

Action.—Extension of the tarso-metatarsus and slight flexion of the fore toes.

Homology.—Uncertainty exists concerning the homology of this muscle. Gadow (1891, p. 185) states that the entire muscle corresponds probably to the *M. triceps surae* of man, and that taken separately the *Pars externa et media* can be compared perhaps to the *M. gastrocnemius*. He states further that the *Pars interna* can be compared to the *M. soleus* or else it corresponds to no muscle of humans. Almost all of the workers on bird musculature have called this three-fold muscle the *M. gastrocnemius;* therefore, it is best to retain the name even though its exact homology is not at present known, and leave it to future investigations to clear up this subject.

Comparison.—The three heads are present in all the birds studied. The P. int. and P. med. are closely associated, usually fusing near the middle of the shank or above.

Pars externa.—Generally the origin is about as in the crow. It is always closely grown together with the lateral femoral arm of the biceps loop. *Gavia* is peculiar in having the origin from a long line down the lateral side of the distal half of the femoral shaft.

Pars media.—This is always the smallest head and in most forms arises about as in *Corvus*. Usually it is closely connected with the*Accessorius semitendinosi*. In *Larus* the middle head is very small and slender, arising by a long and delicate tendon. This part is also very long and slender in *Chen*, and ends in a narrow tendon which inserts into the distal end of the belly of the P. int.

Pars interna.—In the following this head extends around the front of the knee, thus covering the insertion of the sartorius and arising in part from the patellar tendon: *Chen, Cathartes, Pedioecetes, Colinus, Grus, Fulica, Totanus, Larus, Uria.* In *Bubo* and *Otus* the P. int. reaches up somewhat onto the internal condyle of the femur, adjacent to the attachment of the P. med. In *Gavia* and *Colymbus* it arises from a long line down the medial side of the tibia, beginning at the apex of the tibial spine and continuing down to about the middle of the shank. The P. int. is double in *Gavia, Colymbus, Uria,* and *Chaetura,* the semimembranosus inserting between the two heads. In the majority of cases the origin is from the *Caput tibiae* very much as in the crow.

The insertion of the gastrocnemius is subject to considerable differentiation. In the following the whole muscle forms, at the lower part of the shank, a single broad tendon which narrows down toward the heel joint: *Sula, Fregata, Ardea, Cathartes, Falco, Grus, Zenaidura, Coccyzus, Bubo, Otus, Chordeiles, Colaptes, Dryobates, Tyrannus, Corvus. Buteo, Pedioecetes* and *Colinus* are quite similar but the outer and inner edges of the tendon are much thickened, giving the appearance of two heavy tendons united by a thin

fibrous sheet. These two marginal tendons unite shortly above the tibial cartilage.

In many forms there are two entirely separate tendons, the outer from the P. ext. and the inner from the P. int. and med. They fuse farther down the shank. Such a condition is found in *Gavia, Colymbus, Chen, Fulica, Totanus* (Fig. 53), *Larus, Uria,* and *Chaetura.* In *Gavia* the fusion is far down—opposite the tibial cartilage.

The tendon of insertion in *Fregata* passes over the back of the heel joint and then divides into an outer and an inner branch, which insert respectively on the distal end of the outer and inner sides of the tarso-metatarsus. As a result the bundle of flexor tendons passing down the posterior sulcus of the tarsus is not enclosed by the tendon of the Gas. as is usually the case.

M. PLANTARIS (Plan.)

Soleus—Shufeldt (1890, p. 204).
M. plantaris—Gadow (1891, p. 185).

Description (for the crow and raven).—This small slender muscle is confined entirely to the region of the shank. It arises fleshy from the postero-internal side of the proximal end of the tibia, just below the articulation surface for the femur (Figs. 7, 9). The short belly runs distally across the outer surface of the tendon of insertion of the semimembranosus. About one-third the way down the tibio-tarsus it tapers into the long tendon which passes directly down to its insertion on the proximal end of the tibial cartilage, on the inner side (Figs. 23-27). Throughout most of its extent the tendon is closely applied to the inner surface of the *M. gastrocnemius,* between the *Pars media* and *Pars interna;* in fact, if considerable care is not exercised in removing the latter muscle, the tendon of the *M. plantaris* will be removed along with it.

Action.—Helps to extend the tarso-metatarsus.

Homology.—Gadow (1891, p. 186) states that if the *M. plantaris* arises from the femur it is almost fully homologus to the similarly named muscle of man; however, a femoral origin is very rare in birds. Although the homology is somewhat uncertain it seems best to apply the name *M. plantaris* to this muscle.

Comparison.—The plantaris is absent in *Buteo, Chactura, Bubo,* and *Otus,* but is extremely uniform among the various other bird groups. In most cases it is closely applied to the under side of the gastrocnemius, this connection in *Fregata* amounting almost to a fusion. The origin is similar to that in the crow in the following: *Gavia, Colymbus, Fregata, Cathartes, Totanus, Larus, Coccyzus, Colaptes, Dryobates, Tyrannus.* In many the origin extends a little farther down the tibia—about to the distal edge of the insertion of the semimembranosus. This condition is shown by *Sula, Chen, Ardea, Pedioecetes, Colinus, Grus, Fulica, Uria, Zenaidura,* and *Chordeiles.* The belly is slender and exceptionally long in *Coccyzus,* reaching about two-thirds the way down the shank.

Gadow (1891, p. 186) states that this muscle is entirely lacking in all

birds of prey. However, in *Falco* it is not only present but is more powerfully developed than in any other form examined (Figs. 50, 65). The belly reaches almost to the tibial cartilage, the tendon being very short and stout. The origin extends about halfway down the inner side of the tibia. This was observed in all of the falcons available—*F. peregrinus anatum, F. mexicanus,* and *F. sparverius.* In *Cathartes* this muscle shows the typical condition.

Before going into a detailed discussion of the various flexor muscles it might be well to mention something about the manner in which their tendons pass the intertarsal joint. All of the long toe-flexors perforate the tibial cartilage, the exact method being very intricate but very definite for different birds.

In general the most superficial (posterior) position through the intertarsal joint is taken by the Flex. per. d. III, Flex. per. d. IV, and F. p. et p. d. III (Figs. 29-32, 56, 57). Usually these three tendons traverse the tibial cartilage in the same canal. This is the condition in all forms examined with the exception of *Colaptes, Dryobates, Tyrannus,* and *Corvus,* in which the F. p. et p. d. III passes through a separate canal. When the three pass together through the same canal they may be entirely free from one another or, more often, they are bound in a common sheath which greatly reduces their independence of action. The Flex. per. d. III forms the anterior side of this sheath, the edges wrapping posteriorly around the others. In *Colymbus, Totanus, Larus,* and *Coccyzus* the three are not bound together at the tibial cartilage. In the following they are enclosed in a common sheath in addition to passing through the same canal.

Gavia	*Buteo*	*Uria*
Fregata	*Falco*	*Zenaidura*
Sula	*Pedioecetes*	*Chordeiles*
Ardea	*Colinus*	*Chaetura*
Chen	*Grus*	*Otus*
Cathartes	*Fulica*	*Bubo*

The F. p. et p. d. II passes through the tibial cartilage in a special superficial (posterior) canal on the inner side. The Flex. per. d. II is deeply embedded in a separate canal (Figs. 29-32, 56, 57). The most deeply situated flexors in all cases are the F. hal. l. and F. dig. l.

The perforated process shows all degrees of completeness in the various bird groups. In *Cathartes, Buteo, Falco, Uria, Chaetura, Bubo,* and *Otus* there is no true perforated process. The tendons pass down the posterior sulcus of the tarso-metatarsus without traversing bony canals. The two deep flexors may lie in bony grooves, but these are not roofed over with bone. In the following the F. dig. l. alone passes through a completely ossified canal: *Butorides* (Fig. 56), *Chen, Grus, Totanus, Larus, Chordeiles.* Both of the deep flexors lie in bony canals in *Fregata, Sula, Ardea,* and *Coccyzus.* The F. dig. l. and Flex. per. d. II perforate the bone in *Fulica;* the F. dig. l., F. hal. l., and F. p. et p. d. II in *Colymbus* and *Pedioecetes;* the F. dig. l., Flex. per. d. II and F. p. et p. d. II in *Colinus.* In *Zenaidura* all of the flexors perforate the bone except the three superficial ones (Flex. per. d. III, Flex. per. d. IV, and F. p. et p. d. III). The perforated process is completely roofed over

and all the flexor tendons pass through it in *Gavia, Colaptes, Dryobates Tyrannus,* and *Corvus* (Figs. 30, 31).

In determining which tendons pass through bony canals it is necessary to use fully adult specimens, since age greatly affects the degree of ossification.

MM. FLEXORES PERFORATI DIGITI II, III, IV.

As Gadow (1891, p. 186) states, these three muscles belong genetically close together, but since their tendons are entirely independent below, a separate treatment of them seems perfectly proper. This authority further points out that this muscle complex must be regarded as peculiar to birds, since the entire group seems to be present independently neither among reptiles nor mammals (1891, p. 187). In their carneous portions these muscles are very intimately grown together with adjacent muscles; indeed, this is true of almost all the muscles of the shank, the bellies of many being separated only with difficulty. However, in all cases the tendons are very distinct below.

It might be well to add that the insertions of the three perforated and the two perforating and perforated flexors are, in general, not closely circumscribed as with many muscles, but are diffused in a rather confusing manner over an extensive area on the various phalanges of the toes. The insertions shown in the figures are, therefore, only roughly approximate, and indicate only the main points of attachment.

M. FLEXOR PERFORATUS DIGITI II (Flex. per. d. II)

Flexor perforatus indicis primus pedis—Shufeldt (1890, p. 245).
M. flexor perforatus digiti II—Gadow (1891, p. 187).

Description (for the crow and raven).—This small slender muscle lies on the lateral side of the shank between the F. p. et p. d. III in front and the F. hal. l. behind (Figs. 2, 3, 23-28). It has no direct osseous connection above, but originates from the heavy tendon which arises from the posterior side of the external condyle of the femur just distal to the attachment of the P. ext. M. gas. (Fig. 14). This tendon also gives origin to the two perforating and perforated flexors and to the anterior head of the F. hal. l. Furthermore the anterior arm of the tendinous loop for the Bic. fem. makes an attachment anteriorly with the tendon in question.

In addition the Flex. per. d. II arises throughout most of its carneous portion from a fibrous sheet which connects it medially with the bellies of the F. p. et p. d. III and the F. dig. l.

In its middle portion the belly of this muscle is much compressed in an antero-posterior plane. It terminates about two-thirds of the way down the tibio-tarsus in a slender tendon which passes obliquely downward and backward to the tibial cartilage. It perforates this cartilage near the outer side, close to the bone and just behind the tendon of the F. hal. l. (Fig. 29). Upon passing the intertarsal joint it becomes deflected somewhat toward the inner side and passes through the perforated process in its special bony canal, just behind that of the F. dig. l. and in front of that of the F. p. et p. d. II (Figs. 30, 31).

About midway the tarso-metatarsus this tendon switches over the inner side of that of the F. p. et p. d. II, so that lower down their positions are reversed (Figs. 32-37). The insertion is sheath-like and takes place on an extensive area on the under sides of the proximal phalanx of the index digit (Fig. 13). At the point of insertion the tendon is perforated by that of the F. p. et p. d. II and a branch of the F. dig. l.

Action.—Flexion of the index digit.

Homology.—Peculiar to birds (Gadow, 1891, p. 187).

Comparison.—This muscle was found in all birds examined with the exception of *Colymbus* and *Chaetura*. Gadow (1891, p. 188) mentions it as being absent in *Struthio*, corresponding to the absent toe, but does not refer to its absence in any other forms. The second toe is well developed in *Colymbus* and *Chaetura*, yet the muscle is wholly lacking.

The Flex. per. d. II generally consists of a single head which arises out of the *Regio intercondyloidea* in common with other flexor muscles. It is usually connected with the ambiens tendon when this is present, this attachment often taking the form of a small second head of origin. In nearly all birds the belly is deeply situated (Figs. 52, 53), lying directly against the F. dig. l. However, in the passerine birds examined *(Tyrannus* and *Corvus)* the muscle is mostly superficial on the lateral side of the shank (Figs. 1, 24).

In the following the origin is from the *Regio intercondyloidea* and the ambiens tendon:

Gavia	*Buteo*	*Fulica*
Fregata	*Falco*	*Larus*
Sula	*Pedioecetes*	*Totanus*
Chen	*Colinus*	*Zenaidura*
Cathartes	*Grus*	*Coccyzus*

The origin in *Ardea* and *Uria* is from a part of the shaft of the fibula and adjacent flexor muscles; from the external condyle only in *Tyrannus* and *Corvus* (Gadow, 1891, p. 188, gives the origin in Corvidae as being from the *Regio intercondyloidea* only); mainly out of the *Regio intercondyloidea* in *Colaptes* and *Dryobates*. In *Bubo* and *Otus* the origin is by two heads, one from the *Regio intercondyloidea* and the other from the external condyle; both are in company with other muscles. The biceps tendon passes between these two heads.

The insertion is usually on the extreme proximal end of the first phalanx of the index digit. In many birds the attachment is on the outer side of the proximal end of the first phalanx, and the tendon is not very definitely perforated by the two other flexors. The tendon is not perforated at all in *Chen, Cathartes, Buteo, Falco,* and *Uria*. In *Coccyzus, Tyrannus,* and *Corvus* the insertion is on the distal portion of the first phalanx.

Fregata is very peculiar in that just below the perforated process the Flex. per. d. II gives off a strong lateral branch which inserts on the base of the first phalanx of the hallux. Gadow mentions no such attachment for this muscle.

M. FLEXOR PERFORATUS DIGITI III (Flex. per. d. III)

Flexor perforatus medius primus pedis—Shufeldt (1890, p. 242).
M. flexor perforatus digiti III—Gadow (1891, p. 188).

Description (for the crow and raven).—Arises partly out of the intercondyloid region of the femur in company with the Flex. per. d. IV and the posterior head of the F. hal. l. (Figs. 4, 14); however, it arises chiefly from the postero-inner surface of the Flex. per. d. IV, the bellies of these two muscles being closely grown together throughout almost their entire lengths (Figs. 23-28). Well below the middle of the shank the flattened muscle terminates in a strong tendon which passes obliquely outward and downward so as to penetrate the tibial cartilage toward its outer side (Fig. 29). Throughout the region of the heel this wide tendon wraps sheath-like around the anterior side of the tendon of the Flex. per. d. IV; in fact, these two closely associated tendons pass together through a special bony canal in the postero-lateral side of the perforated process (Figs. 30, 31). Shortly below this process the tendon of the Flex. per. d. III is reinforced by the long tendon of the Per. long. In passing down the posterior border of the tarso-metatarsus this tendon shifts obliquely inward around the medial side of the tendon of the F. p. et p. d. III, so that finally just above the toes it comes to lie superficially in the median line (Figs. 32-37). Insertion is on the third toe by a sheath-like tendon which becomes attached to the under sides of the proximal phalanx, and to a more limited extent to the proximal end of the second phalanx (Fig. 13). At the point of insertion the tendon is perforated by that of the F. p. et p. d. III and a branch of the F. dig. l.

Action.—Flexion of the third digit.

Homology.—Peculiar to birds (Gadow, 1891, p. 187).

Comparison.—Present in all forms studied. Usually two-headed, the main one out of the *Regio intercondyloidea* and a more distal head which arises in various ways. When the ambiens tendon is present and well developed the Flex. per. d. III is more or less directly attached to it along with the other two "perforatus" muscles. The muscle is single in *Fregata, Sula, Cathartes, Ardea, Tyrannus,* and *Corvus,* and arises out of the *Regio intercondyloidea.* In *Ardea,* however, there is also an attachment to the shaft of the fibula. The origin in *Chaetura* is from the external condyle in company with the Flex. per. d. IV. There is also a slight attachment to the fibula.

The femoral head is usually fleshy and fused with other flexor muscles, but in *Falco* it arises as a long independent tendon. *Coccyzus* is quite similar. The femoral attachment in *Chaetura* is also by a long tendon.

As Gadow (1891, p. 188) states, the exact attachments of these perforated flexors are hardly to be determined with certainty. The bellies are usually grown together in varied and complex ways. In the following the distal head arises mainly from the other flexor muscles: *Chen, Buteo, Falco, Pedioecetes, Bubo, Otus;* mainly from the shaft of the fibula in *Colymbus* and *Uria;* from the ambiens tendon and the *Caput fibulae* in *Gavia, Colinus, Grus, Fulica, Totanus, Larus, Zenaidura* and *Coccyzus;* from the *Caput fibulae* in *Chordeiles;* from the external condyle in *Colaptes* and *Dryobates.*

In many birds the two bellies unite and only one tendon is formed. In others each head forms a separate tendon, these uniting usually just above the tibial cartilage.

One tendon		Two tendons
Gavia	*Larus*	*Pedioecetes*
Colymbus	*Zenaidura*	*Colinus*
Chen	*Coccyzus*	*Fulica*
Buteo	*Chordeiles*	*Uria*
Falco	*Bubo*	*Colaptes*
Grus	*Otus*	
Totanus	*Dryobates*	

Frequently there is a heavy tendinous *vinculum* (Fig. 74) which, just above the toes, passes downward from the tendon of the Flex. per. d. III, and fuses with that of the F. p. et p. d. III. This firmly binds them together.

Vinculum present		*Vinculum absent*	
Gavia	*Totanus*	*Colymbus*	*Chaetura*
Sula	*Larus*	*Fregata*	*Bubo*
Chen	*Zenaidura*	*Ardea*	*Otus*
Cathartes	domestic duck	*Buteo*	*Colaptes*
Pedioecetes	domestic fowl	*Falco*	*Dryobates*
Colinus	ring-necked pheasant	*Uria*	*Tyrannus*
Grus	domestic pigeon	*Coccyzus*	*Corvus*
Fulica		*Chordeiles*	

This seems to prove conclusively that Gadow and previous writers did not work out all of the leg muscles in any large number of birds, since this vinculum occurs in a great variety of forms, and is so strongly developed that it could hardly be overlooked. Gadow (1891, p. 189) mentions it only for *Pterocles*. The vinculum connecting the two deep flexors has been studied in a large series of birds by Sundevall, Garrod, and others, and it appears certain that if the one connecting these two perforated flexors were widely known, it would have been extensively investigated.

The vinculum under consideration shows very little modification in the birds studied. In some forms it is rather long and slender and in others short and stout. It shows no such complex variations as are exhibited by the similar structure connecting the two deep flexor tendons. Nevertheless it should prove to be of even greater taxonomic significance since it is absent in many groups and present in many others. That between the two deep flexors is present in all groups with the exception of the Passeriformes and *Upupa*.

M. FLEXOR PERFORATUS DIGITI IV (Flex. per. d. IV)

Flexor perforatus annularis primus pedis—Shufeldt (1890, p. 241).
M. flexor perforatus digiti IV—Gadow (1891, p. 190).

Description (for the crow and raven).—This muscle originates above from the intercondyloid region of the femur, in company with the Flex. per. d. III and the posterior head of the F. hal. l. (Figs. 3, 4, 14). Its most extensive surface of origin is from the posterior side of the belly of the F. hal. l., with which it is closely grown together. The long flattened belly terminates a short distance above the malleoli of the tibio-tarsus in a strong tendon which passes

almost through the middle of the tibial cartilage (Figs. 23-29). In this region the tendon of the present muscle is ensheathed anteriorly by the much flattened tendon of the Flex. per. d. III. These two closely associated tendons traverse the perforated process together in their special bony canal, located in the postero-lateral side (Figs. 30, 31). Throughout the length of the tarsometatarsus the tendon of the Flex. per. d. IV maintains its position on the postero-lateral side. Shortly beyond the base of the fourth toe the tendon bifurcates (Figs. 4, 32-37). The short lateral branch inserts on the postero-lateral side of the proximal phalanx, near its distal end; the inner branch encloses sheath-like the branch of the F. dig. l., and inserts on the proximal end of the third phalanx (Figs. 13, 43). Shufeldt's name "annularis *primus* pedis" is, therefore, inappropriate since the most extensive part of the insertion is on the third phalanx. This author has, however, pointed out (1890, p. 242) that this muscle fulfills "the part, too, of a *secundus flexor* of this toe." Nevertheless, I find that this tendon makes almost no attachment to the second phalanx in the crow and raven.

Action.—Flexion of the fourth digit.

Homology.—Peculiar to birds (Gadow, 1891, p. 187).

Comparison.—Present in all forms studied. Arises mainly by one head from the *Regio intercondyloidea,* but in many birds there is also a small lateral head from the *Caput fibulae* or external condyle. This latter portion is mostly tendinous and is frequently attached to the ambiens tendon. It is often rather indefinite but in some, such as *Fulica,* is strongly developed. In the following there is no well defined lateral head: *Gavia, Colymbus, Fregata, Sula, Falco, Uria, Corvus. Gavia* is peculiar in that the femoral attachment extends almost halfway up the shaft of the femur, and, further, the belly reaches almost to the tibial cartilage. The single head in *Falco* is peculiar in coming from the external condyle and *Caput fibulae* instead of from the *Regio intercondyloidea.* In *Chaetura* the single head is also from the external condyle. Gadow (1891, p. 190) gives the origin in the Corvidae as being chiefly from the external condyle. This is wrong as far as the crow and raven are concerned, for in them it arises only from the *Regio intercondyloidea* and other flexor muscles. In addition to the usual origin, *Uria* shows an attachment to a long line down the shaft of the fibula.

All other forms examined show a definite indication of the small lateral head of origin in addition to the main one from the *Regio intercondyloidea.* In some the biceps tendon passes between these two heads, in others laterally to both.

Passes between them		Lateral to both
Ardea	*Totanus*	*Chen*
Buteo	*Larus*	*Zenaidura*
Pedioecetes	*Bubo*	*Coccyzus*
Colinus	*Otus*	*Chordeiles*
Grus	*Tyrannus*	*Colaptes*
Fulica		*Dryobates*

The tendon of insertion is clearly branched in some birds and undivided in others. In the following there is no definite indication of a division: *Gavia,*

Fregata, Buteo, Falco, Pedioecetes, Colinus, Grus, Fulica, Larus, Uria, Chaetura, Coccyzus, Bubo, Otus. In *Coccyzus* the single attachment is on the outer side of the base of the second phalanx, and is not clearly perforated. The tendon of insertion is branched and shows two separate points of attachment in *Sula, Ardea, Chen, Totanus, Zenaidura, Chordeiles, Colaptes, Dryobates, Tyrannus, Corvus.* In these birds the shorter branch usually inserts on the base of the second phalanx and the longer one on the base of the third. The deep flexor ordinarily perforates the longer branch only. However, in *Zenaidura* both are separately perforated. In the woodpeckers, on the other hand, neither is perforated but both branches pass laterally to the deep flexor tendon. This condition was found in all of the woodpeckers examined: *Colaptes auratus, Dryobates villosus, Melanerpes erythrocephalus, Sphyrapicus varius.* Burt (1930, p. 508) gives the insertion in *Ceophloeus pileatus* as being on the basal phalanx. He does not mention a division of the tendon. In *Cathartes* the tendon is trifurcated, inserting mainly on the bases of phalanges II, III, and IV.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI II
(F. p. et p. d. II)

Flexor perforatus indicis secundus pedis—Shufeldt (1890, p. 229).
M. flexor perforans et perforatus digiti II—Gadow (1891, p. 191).

Description (for the crow and raven).—Arises from the external condyle of the femur in company with the anterior head of the F. hal. l., the Flex. per. d. II and the F. p. et p. d. III (Fig. 8). It is fully exposed upon the removal of the *P. ext. M. gastrocnemii.* The belly is small, flattened and spindle-shaped, and terminates about one-third the way down the shank in a thin flat tendon which runs diagonally downward and backward to the tibial cartilage (Figs. 2, 23-28). This tendon becomes much narrowed as it approaches the heel, and passes superficially through the postero-inner side of the tibial cartilage (Fig. 29). Continuing below it traverses the perforated process on the inner side, just behind the tendon of the Flex. per. d. II, and in front of and medial to that of the F. p. et p. d. III (Figs. 30, 31). As explained previously the tendon of the Flex. per. d. II, about midway the tarso-metatarsus, switches around the inner side of the present tendon, so that just above the toes the two have reversed their former positions (Figs. 32-37). Opposite the proximal phalanx of the index digit the tendon of the F. p. et p. d. II perforates that of the Flex. per. d. II, and opposite the base of the second phalanx, is itself perforated by the branch of the F. dig. l. going to the second toe (Figs. 3, 39). It inserts to a limited extent on the distal end of the proximal phalanx, and on the second phalanx, especially on its inner side (Fig. 13).

Action.—Flexion of the index digit.

Homology.—Very uncertain: Gadow (1891, p. 193) states, in speaking of this and the following muscle, that they perhaps represent very imperfectly the *M. soleus* of mammals. From this it seems advisable to regard the two perforating and perforated flexors as being peculiar to birds, at least until such a time as their homologies are better known.

Comparison.—Present in all forms examined. Arises by only one head in all except *Gavia,* in which there are three. It is always superficial after the removal of the external head of the gastrocnemius, and usually lies behind the F. p. et p. d. III, although often overlapping the latter at its postero-proximal end, in *Larus* completely concealing it. The belly is narrow and lies entirely behind the F. p. et p. d. III in *Colymbus* and *Sula.* The origin varies somewhat but is always grown together with underlying muscles. In the great majority of forms the muscle originates from the external condyle and patellar tendon. In *Fregata* it arises mainly from the *Caput fibulae;* from the external condyle, patellar tendon, and lateral edge of the tibial crest in *Ardea, Falco, Fulica,* and *Larus.* In *Larus* the tibial attachment is on the entire anterior crest. Usually the belly is small and weak as in the crow, but it is strongly developed in *Gavia, Colymbus, Pedioecetes, Fulica, Bubo,* and *Otus.* The origin in *Gavia* is by three heads: one from the procnemial spine, one from the external condyle, and a small one from the belly of the F. p. et p. d. III far down the shank. The first two are separated proximally by the insertion of the Il. tib. The third head forms a separate tendon which unites with the main tendon just above the tibial cartilage.

In *Colaptes* and *Dryobates* the insertion is very peculiar; it becomes attached to the inner side of the base of the second phalanx by a slender tendon which is not perforated by the branch from the deep flexor. The same condition was found in *Melanerpes erythrocephalus* and *Sphyrapicus varius.* Burt (1930, p. 506) gives a similar insertion for *Ceophloeus pileatus,* but does not point out the lack of a perforation. The insertion in *Chaetura* is very similar to that in the woodpeckers.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI III (F. p. et p. d. III)

Flexor perforatus medius secundus pedis—Shufeldt (1890, p. 243).
M. flexor perforans et perforatus digiti III—Gadow (1891, p. 192).

Description (for the crow and raven).—This muscle lies on the lateral side of the shank and is fully exposed by the removal of the Per. long. and the *P. ext. M. gastrocnemii* (Figs. 1, 2). Its origin is probably more complex than that of any other muscle of the pelvic limb. It arises partly from the external condyle of the femur in company with the anterior head of the F. hal. l., the Flex. per. d. II, and the F. p. et p. d. II (Fig. 8); also from the lateral side of the anterior crest of the tibia, from the head of the fibula, and from a long narrow line on the lateral side of the slender fibular ligament. In some specimens the origin slightly overlaps the patellar tendon.

The belly of this muscle is intimately grown together with adjacent muscles. About two-thirds of the way down the tibio-tarsus it ends in a strong tendon which runs superficially through the posterior side of the tibial cartilage (Figs. 23-29). From here it switches somewhat to the inner side so that it passes through the perforated process in a special bony canal near the postero-inner margin (Figs. 30-37). On the way down the posterior side of the tarso-metatarsus the tendon gradually shifts toward the outer side, so as to arrive at the base of the third toe. Just above the base of the toe the tendon

passes laterally under that of the Flex. per. d. III. It perforates the latter tendon opposite the proximal phalanx, and opposite the second phalanx is itself perforated by the branch of the F. dig. l. going to the third digit. Insertion is on the distal end of the second phalanx and on the proximal end of the third (Figs. 3, 13, 41).

Action.—Flexion of the third toe.

Homology.—Very uncertain. See foregoing muscle.

Comparison.—Present in all forms. One-headed and usually much larger than the preceding muscle. Arises generally from the lateral edge of the tibial crest, from the patellar tendon, the external condyle, and the *Caput fibulae;* in many birds also from the fibular shaft, often for a considerable distance.

Origin including fibular shaft		Not connected with fibular shaft	
Gavia	*Zenaidura*	*Chen*	*Larus*
Colymbus	*Coccyzus*	*Buteo*	*Chordeiles*
Fregata	*Colaptes*	*Pedioecetes*	*Bubo*
Sula	*Dryobates*	*Colinus*	*Otus*
Ardea	*Tyrannus*	*Grus*	
Cathartes	*Corvus*	*Fulica*	
Falco		*Totanus*	
Uria			

There is no connection with the anterior tibial crest in *Uria, Bubo,* and *Otus.* Gadow (1891, p. 193) gives the origin in the Corvidae as being from the external condyle and *Caput fibulae.* He does not mention the attachment to the tibial crest and shaft of the fibula. In *Chaetura* the origin is from the fibula only.

The insertion shows no important modifications other than the vinculum connecting this tendon with that of the Flex. per. d. III as already described under the discussion of the latter muscle. Gadow (1891, p. 193) states that in the Ratitae, fowls, and *Pterocles,* the tendon of this muscle is connected by a vinculum with the Flex. per. d. III just above the *intertarsal joint.* No such condition was encountered in this investigation.

M. FLEXOR DIGITORUM LONGUS (F. dig. l.)

Flexor perforans digitorum profundus—Shufeldt (1890, p. 246).
M. flexor profundus s. perforans—Gadow (1891, p. 193).

Description (for the crow and raven).—This powerful muscle is the most deeply situated of all the muscles on the posterior side of the shank—lying immediately next to the bone (Figs. 4, 5, 23-28). It arises by two distinct heads, the more posterior of which attaches itself by means of fleshy fibers to the posterior side of the external condyle of the femur (Fig. 14). This relatively small head fuses, just above the insertion of the Bic. fem., with the much larger head which arises fleshy from a very extensive area on the posterior surface of the tibia and fibula. This great area of attachment extends down the tibio-tarsus for more than two-thirds of its entire length (Fig. 15). At the extreme proximal end of the large anterior head there is a slight notch which might be construed as being a division of the muscle into a total of three heads.

Throughout most of its length the belly of this muscle is divided in the postero-median line by a tendinous band which is continuous below with the tendon. This gives the muscle a pennate structure. About three-fourths of the way down the shank the muscle changes into the powerful tendon which penetrates the tibial cartilage close to the bone and slightly on the inner side (Fig. 29). Below this it penetrates the perforated process in the same relative position, in a special bony canal (Figs. 30, 31). Down the posterior sulcus of the tarso-metatarsus the tendon gradually shifts to the outer side, so that just above the toes this tendon and that of the F. hal. l. have reversed their former positions (Figs. 32-37). Opposite the middle of the tarso-metatarsus the tendon of the F. dig. l. becomes highly ossified for a considerable distance. Shortly above the bases of the toes it divides into three branches, one of which passes to each of the fore toes (Fig. 5). These run distally close to the phalanges and perforate the tendons of the other toe flexors as already described (Figs. 39-45). The insertion of each of these tendons is double, the smaller branch becoming attached to the penultimate phalanx and the larger to the base of the unguinal phalanx (Fig. 13). I find this double insertion of the deep flexor tendons to be constantly present in the crow, but there is no reference to such a condition in the literature at my disposal. The same double insertion also occurs in the raven.

Action.—Flexion of the fore toes.

Homology.—Gadow (1891, p. 195) states that this muscle corresponds to the *M. flexor longus digitorum* of mammals. According to the BNA this becomes the *M. flexor digitorum longus.*

Comparison.—Present in all birds. The origin is usually from an extensive area on the posterior side of the tibia and fibula, from the proximal end downward for a variable distance but ordinarily extending beyond the middle of the shank. In most cases the belly is divided at the proximal end by deeply situated nerves and blood vessels. In such a typically developed condition, which occurs in the vast majority of birds, there is no connection with the femur. *Colaptes* and *Dryobates* differ slightly in lacking any connection with the *Caput fibulae*. *Tyrannus* and *Corvus* are unique in having two very distinct heads of origin, as already described for the crow. This condition is apparently peculiar to the Passeriformes. In *Buteo* this muscle is very powerfully developed, being extensively visible superficially on the lateral side of the shank. In addition to the main head there is a tendinous connection with the lateral side of the anterior tibial crest. The origin in *Pedioecetes* is double as in *Buteo* but otherwise the belly is typical. *Bubo* and *Otus* have the F. dig. l. extremely large and powerful. The belly is visible superficially for the entire length of the shank on both the outer and inner sides (Fig. 51). The origin is by three heads: an outer one from the *Caput fibulae*, the main head as usual, and an inner one from the medial surface of the *Caput tibiae* and much of the shaft below this. The proximal end of the inner head lies anterior to the insertion of the semimembranosus.

Usually the tendon of the F. hal. l. lies in a lateral position at the heel joint as in the crow (Plate 26), but in the following it lies directly pos-

terior to the tendon of the F. dig. 1: *Fregata, Buteo, Falco, Chaetura, Bubo, Otus*. In these both tendons are very large.

As Sundevall, Garrod, and others have shown, the two deep flexor tendons are connected in the region of the tarso-metatarsus in all groups of birds with the exception of the Passeriformes and *Upupa*. In *Tyrannus* and *Corvus* the condition is like that already described for the crow. In the following the two tendons fuse into one, usually near the middle of the tarso-metatarsus: *Gavia* (Fig. 71), *Colymbus, Fregata* (Fig. 72), *Chen, Cathartes, Larus, Uria, Chordeiles, Chaetura*. The common tendon divides below into four branches, one for each toe, in *Fregata, Cathartes, Chordeiles,* and *Chaetura*. In *Chen* (also in *Mergus merganser americanus)* the F. hal. l. sends off, just above the point of fusion, a small branch to the hallux. The common tendon divides into three branches, one for each fore toe, in *Gavia, Colymbus, Larus,* and *Uria*. In these there is no branch to the hallux, which is very small in all except *Uria,* in which it is absent.

In most birds the two deep flexor tendons cross near the middle of the tarso-metatarsus as already described for the crow. At or below the point of crossing a tendinous *vinculum* of variable size and extent passes down from the tendon of the F. hal. l. and fuses with that of the F. dig. l., thus firmly binding them together and destroying their independence of action (Figs. 69, 70, 73). This vinculum occurs in the following:

Sula	*Colinus*	*Coccyzus*
Ardea	*Grus*	*Bubo*
Buteo	*Fulica*	*Otus*
Falco	*Totanus*	*Colaptes*
Pedioecetes	*Zenaidura*	*Dryobates*

Buteo and *Falco,* in addition to having a strong and extensive vinculum as in the owls, have a stout connection between the F. hal. l. and the branch of the main flexor going to the index digit. In conformity with this the deep tendon to the second toe is about twice as large as the branches to the third and fourth toes. This condition has been described by Garrod (1875, p. 343) for several genera of Falconiformes.

In *Otus* the tendon of the F. dig. l. divides into two near the upper end of the tarso-metatarsus (Fig. 59). The inner branch supplies digits two and three, the outer branch digit four. These two tendons are closely connected.

Colaptes and *Dryobates* show a very peculiar modification of the two deep flexors. The F. dig. l. supplies only the third toe. The F. hal. l trifurcates, sending a branch to digits one, two, and four (Fig. 73). Garrod (1875, p. 346), Gadow (1891, p. 195), and Burt (1930, p. 507) have reported this for the woodpeckers and their allies.

The small fibro-elastic slips from the tendons of the F. dig. l., such as have already been described for the crow, occur very commonly among birds. In some species certain digits are supplied with as many as three, all inserting on different phalanges. Frequently these small branches are very indefinite and they are probably of little, if any, taxonomic importance.

M. FLEXOR HALLUCIS LONGUS (F. hal. l.)

Flexor longus hallucis—Shufeldt (1890, p. 232).

M. flexor hallucis longus—Gadow (1891, p. 197).

Description (for the crow and raven).—This is one of the most powerful muscles of the leg, and is located directly behind the F. dig. l. It arises by two heads which are separated by the tendons of the Bic. fem. The small anterior head arises from the external condyle of the femur in company with the Flex. per. d. II and the two perforating and perforated flexors (Figs. 3, 8). The posterior head is much larger and arises from the intercondyloid region of the femur in common with the perforated flexors for the third and fourth toes (Fig. 14). Opposite the tendinous loop for the Bic. fem. a tendinous band connects the anterior and posterior heads of this muscle. This might be considered a third or middle head. Shortly below the tendon of the Bic. fem. the anterior and posterior heads unite to form the large belly, which passes directly down the back of the shank in intimate connection with several adjacent flexor muscles. Near the lower end of the shank the muscle connects with its powerful tendon which perforates the tibial cartilage deeply, on its outer side (Figs. 23-29). Below this it traverses the perforated process in the same relative position, in a special bony canal (Figs. 30, 31). On passing down the posterior sulcus of the tarso-metatarsus the tendon crosses gradually over the back of the tendon of the F. dig. l., so as to reach the base of the first metatarsal bone. As already pointed out this crossing over of the two deep flexor tendons causes them to reverse their relative positions below (Figs. 32-37).

Upon reaching the inner side of the tarso-metatarsus the tendon in question passes between the first and second metatarsals, at which point it perforates the greatly enlarged and sheath-like tendon of the F. hal. brev. Beyond the base of the proximal phalanx of the hallux it continues to its insertion, which is bifurcated in much the same manner as the tendons of the F. dig. l. already described. Insertion is by a small branch on the distal end of the proximal phalanx, and by a large branch on the under side of the unguinal phalanx (Figs. 4, 13, 17, 38). I have found no reference in the literature to this double insertion.

Action.—Flexion of the hallux; however, as has already been described, several of the flexor muscles of the shank are more or less intimately fused above, and it is probable that these muscles cannot act entirely independently of one another.

Homology.—Corresponds to the similarly named muscle of man (Gadow, 1891, p. 197).

Comparison.—The flexor hallucis longus is present in all forms. It is usually much weaker than in the crow, but in the hawks and owls especially it is very powerful.

Strongly developed	Very weak
Fregata	*Gavia*
Buteo	*Chen*
Falco	*Totanus*
Chaetura	*Larus*
Bubo	*Uria*
Otus	*Coccyzus*
Colaptes	
Dryobates	
Tyrannus	
Corvus	

In most forms the origin is by a single head from the *Regio intercondyloidea*, usually closely fused with the perforated flexors. The following is a synopsis of the forms in which the muscle is two-headed:

Buteo, Falco—From the postero-lateral side of the femoral shaft immediately above the external condyle; from the *Regio intercondyloidea* and joint capsule.

Bubo, Otus—Main head from the *Regio intercondyloidea;* a small anterior head from the capsular ligament on the posterior side of the knee joint.

Colaptes, Dryobates—From the *Regio intercondyloidea;* from the *Caput fibulae* and much of the fibular shaft.

Tyrannus, Corvus—Main head from the *Regio intercondyloidea;* a small head from the external condyle.

In *Tyrannus* and *Corvus* the biceps tendon passes between the two heads of the F. hal. l. In all others the entire muscle is medial to the biceps.

The tendon of insertion in many birds perforates the sheath-like tendon of the F. hal. brev., very much as in the crow. This is clearly the case in the following:

Fregata	*Pedioecetes*	*Colaptes*
Sula	*Colinus*	*Dryobates*
Ardea	*Zenaidura*	*Tyrannus*
Cathartes	*Coccyzus*	*Corvus*

Owing to the minute size of the F. hal. brev. in the crow this perforation is difficult to demonstrate. However, in *Tyrannus*, in which the F. hal. brev. is well developed, the perforation is very easily observable.

The small fibro-elastic branch from the main tendon, which has been described for the crow, occurs in most forms. It is probably of little or no importance taxonomically.

For a more detailed treatment of the insertion of the F. hal. l. see the foregoing muscle.

M. POPLITEUS (Pop.)

M. popliteus—Gadow (1891, p. 176).

Description.—(for the great horned owl—*Bubo virginianus*).—This short thick muscle is fleshy throughout and arises from the posterior border of the neck of the fibula, immediately above the insertion of the Bic. fem. Insertion is on the posterior surface of the shaft of the tibia almost directly opposite the origin (Fig. 66). The muscle is somewhat triangular in shape with the base on the fibula and the apex on the tibia. It is only about as long as the width of the tibial shaft.

The *M. popliteus* is deeply situated against the bone and is visible only after the removal of the other posterior muscles of the shank.

Action.—Draws the fibula slightly toward the tibia.

Homology.—Homologous to the *M. popliteus* of man—Gadow (1891, p. 209).

Comparison.—The popliteus is present in all forms examined with the exception of *Chaetura, Colaptes, Dryobates, Tyrannus,* and *Corvus.* It is always small and simple and in most forms shows about the same condition as in *Bubo.* It is comparatively weak and narrow in *Sula, Chen, Larus,* and *Chordeiles.* In *Colymbus* it is wide and flat, being almost twice as wide as long. Usually the fibular and tibial attachments are directly opposite as in *Bubo,* but in the following the muscle runs diagonally from the fibula down to a more distal point on the tibia: *Sula, Chen, Totanus, Larus, Chordeiles.*

M. EXTENSOR HALLUCIS LONGUS (Ext. hal. l.)

Extensor hallucis brevis—Shufeldt (1890, p. 218).
M. extensor hallucis brevis—Gadow (1891, p. 197).

Description (for the crow and raven).—This is one of the smallest muscles of the leg. It arises fleshy from the antero-internal border of the proximal end of the tarso-metatarsus (Figs. 9, 10). The belly is very long and slender and extends down the antero-internal side of the tarso-metatarsus for more than half the length of that bone (Figs. 5, 30-34). Below, the muscle terminates in a weak and flattened tendon which runs close to the bone, obliquely backward along the posterior side of the first metatarsal (Figs. 35-37). It continues distally along the dorsal side of the hallux to its insertion on the distal phalanx (Figs. 10, 38).

In these two birds the tendon passes through a heavy fibro-elastic mass of tissue on the dorsal side of the hallux near the distal end of the proximal phalanx (Figs. 17, 38). This tissue and the tendon of the Ext. hal. l. insert together on the base of the unguinal phalanx. The structure of this elastic tissue is such that it functions as an extensor of the claw and, therefore, as an antagonist of the F. hal. l. When the tension on the big flexor tendon is relaxed this elastic ligament automatically elevates the claw. It appears that this spring-like device serves the purpose of compensating for the lack of a strong hallucial extensor muscle. I have found no reference to this structure in the literature on bird muscles.

Action.—Weak extension of the hallux.

Homology.—Gadow (1891, p. 198) states that this muscle corresponds to the *M. extensor hallucis proprius* of mammals and reptiles. The BNA name for this muscle is the *M. extensor hallucis longus.*

Comparison.—The Ext. hal. l. is one of the most variable of the short toe-muscles. It is usually one-headed and follows the same course as in the crow. No trace of it was found in *Gavia, Colymbus,* and *Uria* (hallux absent). In many forms the origin is from most of the length of the tarso-metatarsus, and

the muscle is at least partly fleshy all the way to the base of the hallux. This condition is found in the following:

Fregata	*Cathartes*	*Grus*
Sula	*Pedioecetes*	*Fulica*
Ardea	*Colinus*	*Chordeiles*

In *Larus* and *Sterna antillarum* there are two widely separated heads of origin: a very small belly arises from the anterior side of the tarso-metatarsus, adjacent and medial to the insertion of the Tib. ant. This sends down a long slender tendon very much as in the crow. The larger distal head arises from the posterio-medial edge of the tarso-metatarsus, below the middle of this bone; also in part from the small Met. I. The tendon of the long head merges with the belly of the short head near the base of the hallux.

In *Chen* and *Totanus* (Fig. 61) the muscle is short and weak, being limited to the distal half of the tarso-metatarsus. The origin in these birds is from the postero-medial side and has no connection with the anterior surface of the tarso-metatarsus. In the following the origin is from the antero-proximal side only: *Buteo, Falco, Coccyzus, Colaptes, Dryobates, Tyrannus, Corvus.*

The muscle is very peculiar in *Zenaidura,* being double almost all the way. The long head arises from the antero-medial side of the proximal end of the tarso-metatarsus, and inserts as usual on the base of the bony claw. The short head arises from the postero-medial side of the bone and inserts by an independent tendon on the outer side of the hallux, near the base of the proximal phalanx. *Columba livia* shows the same condition.

In *Bubo* and *Otus* (Fig. 55) this muscle arises by two heads, a small one from the proximal end of the tarso-metatarsus on the antero-medial side, and a much larger head which has no connection with the tarso-metatarsus, but arises from the anterior surface of the internal malleolus of the tibio-tarsus and the adjacent fibrous loop for the Ext. dig. l. The two bellies unite below and only one tendon is formed.

The Ext. hal. l. is very powerful in *Buteo* and originates by two heads from the antero-proximal surface of the tarso-metatarsus. The outer head passes lateral to the tendon of the Tib ant. The medial head is large and wraps sheath-like around the tendon of the Ext. dig. l. The two form short tendons which fuse a little above the middle of the tarso-metatarsus. *Falco* (Fig. 54) differs from *Buteo* in that the medial head does not form a sheath about the tendon of the Ext. dig. l.

The insertion in some birds is mainly on the base of the proximal phalanx of the hallux, but in all cases a tendon passes out to the bony claw. Gadow (1891, p. 198) is therefore wrong in stating that the insertion is on the base of the proximal phalanx. In many forms, as in the crow, the insertion is entirely on the base of the unguinal phalanx. In the following the insertion is mainly on the base of the proximal phalanx: *Fregata, Sula, Grus, Fulica, Totanus, Larus.*

M. EXTENSOR PROPRIUS DIGITI III (Ext. pro. d. III)

M. extensor proprius digiti III—Gadow (1891, p. 199).

Description (for the great horned owl—*Bubo virginianus*).—Arises fleshy from an extensive area on the middle of the anterior surface of the tarso-metatarsus, extending down almost the entire length of that bone (Figs. 55, 59, 63). Proximally the muscle lies lateral to the tendon of insertion of the Tib. ant. Insertion is on the dorsal side of the proximal end of the first phalanx of the third digit.

Above, the Ext. pro. d. III is intimately associated with the more laterally situated Ext. brev. d. IV.

Action.—Extension of the third toe.

Homology.—Gadow (1891, p. 199) states that this muscle corresponds imperfectly to the dorsal *Mm. interossei* of mammals.

Comparison.—Although Gadow gives two short extensors for the third digit, only one was found in this investigation. In *Fregata, Grus, Tyrannus,* and *Corvus* no short muscle to the third toe was detected. In *Gavia, Colymbus, Cathartes,* and *Chaetura* it is vestigial. It is well developed in the following and extends along most of the length of the tarso-metatarsus:

Ardea	*Zenaidura*	*Otus*
Butorides	*Coccyzus*	*Colaptes*
(Fig. 60)	*Bubo*	*Dryobates*

Burt (1930) does not give this muscle for the woodpeckers. Nevertheless, it is well developed in all the woodpeckers examined—*Colaptes auratus, Dryobates villosus, Melanerpes erythrocephalus,* and *Sphyrapicus varius.*

In *Buteo* and *Chordeiles* the Ext. pro. d. III is confined to the distal half of the tarso-metatarsus. It is very short and weak in the following, being limited to the distal end of the tarso-metatarsus:

Sula	*Falco*	*Colinus*	*Totanus*
Chen	*Pedioecetes*	*Fulica*	*Uria*

In all cases the insertion is on the base of the proximal phalanx. Insertion is on the antero-*medial* side of the base in *Colaptes* and *Dryobates.*

M. EXTENSOR DIGITORUM BREVIS

According to Gadow (1891, p. 209) the following three muscles correspond to the *M. extensor digitorum brevis* of mammals: Ext. brev. d. III, Ext. brev. d. IV, and Abd. dig. II.

M. EXTENSOR BREVIS DIGITI III (Ext. brev. d. III)

M. extensor brevis digiti III—Gadow (1891, p. 199).

Description.—Gadow describes this muscle about as follows:

> This little muscle is for the most part overlooked in describing the short toe extensors. It arises rather fleshy from the dorsal surface of the distal fourth or fifth of the tarso-metatarsus. On the fibular side it is bounded by the tendon of the *M. ext. proprius s. medius dig. III.* It inserts with a broad short tendon on the proximal dorsal border of the base of Phal. I, Dig. III.

Action.—Weak extension of the third toe.

Homology.—According to Gadow (1891, p. 209) this muscle represents a part of the *M. ext. brevis dig.* of man. However, as he points out, the few muscles of the strongly varied bird foot can be but very imperfectly compared with the numerous short toe-muscles of the other vertebrates.

Comparison.—In no case was more than one short extensor found attached to the third toe. Gadow, however, gives two: *M. extensor proprius digiti III* and *M. extensor brevis digiti III.* He states that both are well developed and entirely independent of one another in the Ratitae. This condition apparently does not occur in any other group of birds. It seems probable that the name *M. extensor brevis digiti III* should be discarded as a synonym of the *M. extensor proprius digiti III.* The former name was introduced by Gadow while the latter had been used by previous writers. It is not uncommon for a muscle to be double in certain restricted groups of birds, but this is no valid argument for the use of two muscle names.

M. EXTENSOR BREVIS DIGITI IV (Ext. brev. d. IV)

M. extensor brevis digiti IV—Gadow (1891, p. 200).

Description (for the great horned owl—*Bubo virginianus*).—This muscle arises fleshy from the antero-outer side of the tarso-metatarsus, from the proximal end to a point about two-thirds the way down the bone. It is bounded medially by the Ext. pro. d. III with which it is in intimate contact proximally. Distally the strong tendon passes into the outer inter-metatarsal space (erroneously called "intertarsal" space by Gadow—1891, p. 201) on the anterior side of the tarso-metatarsus, and inserts on the inner side of the proximal phalanx of the fourth toe (Figs. 63, 55, 59). No lateral arm from the tendon is present (as described by Gadow—1891, p. 201).

Action.—Extension and adduction of the fourth toe.

Homology.—This muscle, together with the preceding and the following, corresponds to the *M. extensor digitorum brevis* of mammals (Gadow—1891, p. 201).

Comparison.—This is one of the most uniform of the foot muscles. It is absent in *Colaptes, Dryobates, Tyrannus,* and *Corvus.* In most forms it is well developed and extends almost the entire length of the tarso-metatarsus. In *Colymbus* the belly is reduced to a thin sheet of connective tissue which probably has no power of contraction, although the tendon is well developed.

In *Fregata* the muscle is peculiar in having two heads of origin: the main one arises from the proximal half of the tarso-metatarsus on the antero-lateral side; the medial belly arises as a continuation of a branch from the tendon of the Tib. ant., also from the middle of the anterior side of the distal half of the tarso-metatarsus. The two heads unite and only one tendon is formed.

The insertion in all forms is on the medial side of the base of the proximal phalanx. Before inserting the tendon passes under a bony bridge in the outer intermetatarsal space in all except *Bubo* and *Coccyzus.* The space in

Bubo is roofed over with fibrous connective tissue, but in *Coccyzus* it is not covered at all, hence the very stout tendon is superficial throughout its course.

M. ABDUCTOR DIGITI II (Abd. dig. II)

M. abductor digiti II—Gadow (1891, p. 201).

Description (for the great horned owl—*Bubo virginianus*).—This short muscle arises fleshy from the dorso-medial surface of the distal fourth of the tarso-metatarsus, and from the adjacent first metatarsal bone. It inserts by a broad tendon on the medial side of the proximal end of *Phal I. Dig. II* (Fig. 63).

Action.—Abduction of the second toe.

Homology.—Corresponds to a part of the *M. extensor digitorum brevis* of mammals (Gadow—1891, p. 209).

Comparison.—Absent in *Colaptes, Dryobates, Tyrannus,* and *Corvus.* Usually the muscle is short and stout as in *Bubo,* but in *Buteo* it extends almost the entire length of the tarso-metatarsus, the origin being from the proximal two-thirds. In *Gavia* and *Colymbus* the Abd. dig. II is reduced to a thin tendinous sheet and is probably incapable of contraction. The belly reaches up to the middle of the tarso-metatarsus in *Fregata, Uria, Zenaidura,* and *Coccyzus.* In most cases the origin is partly from Met. I but in the following there is no connection with this bone: *Ardea, Buteo, Larus, Uria* (Met. I absent), *Zenaidura, Chordeiles,* and *Chaetura.* The origin in *Falco* is almost wholly from the first metatarsal. The insertion in all cases is on the medial side of the proximal phalanx, near its base.

M. FLEXOR HALLUCIS BREVIS (F. hal. brev.)

Flexor brevis hallucis—Shufeldt (1890, p. 256).
M. flexor hallucis brevis—Gadow (1891, p. 202).

Description (for the crow and raven).—This is the smallest muscle of the pelvic appendage in the species under discussion. It arises from a small area on the postero-internal side of the tarso-metatarsus, near the proximal end of that bone (Figs. 9, 13). The minute belly is hardly one-seventh of the length of the tarso-metatarsus (Fig. 6). The extremely delicate tendon runs down superficially on the inner side of the bundle of tendons which passes down the posterior sulcus of the tarso-metatarsus (Figs. 32-37). This tendon is so small that it can be demonstrated only with difficulty. Farther down it passes, in company with the F. hal. l., into the space between the first and second metatarsal bones. At this point the tendon of the present muscle becomes enormously enlarged so as to enclose sheath-like the large tendon of the main flexor (Fig. 17). This fibro-cartilaginous sheath rides over the distal trochlea of the first metatarsal bone and inserts on the base of the proximal phalanx of the hallux (Fig. 13); however, it is also attached to the sides of the distal end of the first metatarsal.

As Gadow (1891, p. 202) has pointed out, the F. hal. brev. behaves as a "flexor perforatus" of the hallux.

Shufeldt overlooked this small muscle in the raven; nevertheless it is present in that bird and has the same structure as in the crow, except that it is much larger, corresponding to the much larger size of the raven. However, Shufeldt (1890, p. 256) described it in the road-runner *(Geococcyx californianus),* but did not mention anything about its tendon being perforated by that of the F. hal. l.

Action.—A weak accessory to the F. hal. l. in flexing the hind toe.

Homology.—Gadow (1891, p. 203) states that this muscle corresponds to the similarly named one of man.

Comparison.—This muscle is subject to considerable modification in the different taxonomic groups. No trace of it was found in *Gavia* and *Uria* (hallux absent). It arises from the postero-medial surface of the tarso-metatarsus as indicated below.

1. From the proximal end almost or quite to the base of the hallux:

Fregata	*Cathartes*	*Zenaidura*
Sula	*Pedioecetes*	*Chordeiles*
Ardea	*Colinus*	*Chaetura*

2. From about the proximal third or half:

Buteo	*Fulica*	*Coccyzus*
Falco (Fig. 54)	*Totanus* (Fig. 57)	*Bubo*
Grus	*Larus*	*Otus* (Fig. 55)

3. From a very small area near the perforated process:

Colymbus	*Dryobates*	*Tyrannus*
Colaptes		*Corvus*

The F. hal. brev. is usually single throughout but in several forms the tendon, and even part of the belly, is double. The following show a definite division of the tendon, at least at the lower end:

Ardea	*Totanus*	*Otus*
Buteo	*Larus*	(Fig. 59)
Fulica	*Bubo*	

In *Ardea* the tendon is divided only for a short distance above the insertion. The two tendons fuse again distally in *Ardea* and *Buteo,* consequently there is only one point of insertion. They remain separate and insert at different points in *Fulica, Totanus, Larus, Bubo,* and *Otus.* The distal end of the belly also is divided in *Fulica, Bubo,* and *Otus.*

In many birds the tendon of insertion is not perforated by the deep flexor tendon; in others such a perforation occurs, the tendon of the F. hal. brev. wrapping sheath-like around that of the F. hal. l. for a short distance.

Not perforated by F. hal. l.		Perforated by F. hal. l.	
Buteo	*Larus*	*Fregata*	*Zenaidura*
Falco	*Chordeiles*	*Sula*	*Coccyzus*
Grus	*Chaetura*	*Ardea*	*Colaptes*
Fulica	*Bubo*	*Cathartes*	*Dryobates*
Totanus	*Otus*	*Pedioecetes*	*Tyrannus*
		Colinus	*Corvus*

In all cases the insertion is on the base of the proximal phalanx of the hallux.

M. ADDUCTOR DIGITI II (Add. d. II)

M. adductor digiti II—Gadow (1891, p. 203).

Description (for the great horned owl—*Bubo virginianus*).—Arises mostly fleshy from about the proximal third of the posterior sulcus of the tarso-metatarsus. Below, the wide flat tendon runs straight down the middle of the posterior sulcus to the groove between metatarsals II and III (Figs. 62, 47, 51). It passes into this groove and inserts on the outer side of the extreme base of *Phal. I, Dig. II*. At the proximal end the belly is bounded laterally by the Abd. d. IV and medially by the F. hal. brev.

Action.—Adduction and flexion of the second toe.

Homology.—According to Gadow (1891, p. 209) the homologue of this muscle in other vertebrate classes is not known.

Comparison.—Absent in *Pedioecetes, Colaptes, Dryobates, Tyrannus,* and *Corvus*. In the following the Add. d. II arises near the proximal end of the tarsus, usually immediately below the perforated process, the tendon being, consequently, very long:

Gavia	*Falco*	*Coccyzus*
Colymbus	*Totanus*	*Bubo*
Cathartes	*Larus*	*Otus*
Buteo	*Uria*	

In *Fregata, Sula, Grus, Fulica, Zenaidura, Chordeiles,* and *Chaetura* the origin extends from the perforated process to the lower end of the tarso-metatarsus. The muscle is confined to the distal half or less of the tarso-metatarsus in *Ardea, Chen,* and *Colinus*. In *Phasianus colchicus torquatus* it is very short, being limited to the distal fourth.

The insertion in all cases is on the lateral side of the base of the proximal phalanx.

M. LUMBRICALIS (Lumb.)

M. flexor brevis digiti III—Gadow (1891, p. 204).

Description (for the green heron—*Butorides virescens*).—This peculiar little muscle arises from the tendons of insertion of the F. dig. l. and the F. hal. l., beginning about one-third the way down the tarso-metatarsus and extending to the bases of the fore toes. Distally the muscle becomes gradually wider before inserting partly tendinous on the joint pulley and capsule at the bases of the third and fourth toes. Throughout its entire length the *M. lumbricalis* is closely attached to the tendons of the two muscles mentioned above, forming more or less of a sheath about them (Fig. 60).

Action.—Meckel (*vide* Gadow—1891, p. 204) considered this muscle as serving to draw the joint pulley behind in order to protect it from pinching

during the bending of the toes. It perhaps also tends to flex the third and fourth digits.

Homology.—Corresponds to one of the *Mm. lumbricales* of mammals (Gadow—1891, p. 204).

Comparison.—This muscle is often very small and rudimentary, hence it is difficult to determine whether it is absent or simply vestigial. It can be studied to the best advantage in fresh, unpreserved specimens in which it appears pinkish in color. In preserved material it is often so faded that it might easily be mistaken for connective tissue. In the following the lumbricalis is well developed and fleshy: *Ardea, Butorides, Zenaidura, Coccyzus, Chordeiles,* and *Chaetura.* Of these it is strongest in *Coccyzus* and *Chordeiles.* In the former it arises from the tendon of the F. dig. l., beginning about one-third of the way down the tarso-metatarsus. Insertion is on the joint pulley for the third toe. In *Chordeiles* this is a clearly defined, compact little muscle, arising by a wide tendon from the anterior surface of the combined deep flexor tendon, just above the division into four branches. The stout belly inserts as usual on the cartilaginous joint pulley for the third digit. In all other forms examined this muscle is either absent or very feebly developed.

M. ADDUCTOR DIGITI IV (Add. d. IV)

M. adductor digiti IV—Gadow (1891, p. 204).

Gadow is apparently the only writer who has mentioned this muscle. A free translation of his description is about as follows:

> This muscle, which is not mentioned in the literature, I have found in only very few birds. In *Rhea* (not seen in the remaining Ratitae) it arises as a very thin muscle fibularly beside the *M. abductor dig. II* * and is partly grown together with the *M. abductor dig. IV.* bounding it laterally. Its tendon goes through the *Spatium intertarsale externum* to the tibial side of the Basis phal. I and adducts the outer toe besides slight plantar flexion.
>
> In *Bucorvus* it arose from the distal end of the tarsus; in *Ramphastus* it was still shorter and useless.

Gadow does not give the homology, this being apparently unknown.

Comparison.—This is the most poorly defined and rudimentary of all the muscles of the pelvic extremity, consequently it is best studied in fresh, unpreserved material. It was found to be well developed and fleshy only in *Phasianus colchicus torquatus.* In this bird it arises fleshy from about the distal fourth of the posterior surface of the tarso-metatarsus, lying between the Add. dig. II and the Abd. d. IV. The little belly inserts mainly on the joint pulley for the third toe, but also sends a short tendon into the outer inter-metatarsal space. This inserts on the medial side of the base of the proximal phalanx of the fourth toe.

In *Grus, Chen,* and a few other forms this muscle is apparently represented by a small fibro-elastic ligament.

M. ABDUCTOR DIGITI IV (Abd. d. IV)

M. abductor digiti IV—Gadow (1891, p. 205).

Description (for the great horned owl—*Bubo virginianus*).—Arises fleshy

* This is a typographical error. It should read: *M. adductor digiti II.*

from the posterior side of the postero-external ridge of the tarso-metatarsus, from the proximal end almost to the distal end (Figs. 62, 55, 59). The long tendon inserts on the antero-outer side of the base of *Phal. I, Dig. IV*. The belly is bounded medially by the Add. d. II and the bundle of flexor tendons which passes down the posterior sulcus of the tarso-metatarsus.

Action.—Abduction of the outer toe.

Homology.—Gadow (1891, p. 209) does not give the homology of this muscle and apparently nothing is known concerning it.

Comparison.—Present in all species studied. In the vast majority of forms the origin is from a long, narrow line extending down the postero-lateral side of almost the entire length of the tarso-metatarsus. It is very stout in *Fregata* and *Sula*, but in *Gavia, Colymbus, Colaptes, Dryobates, Tyrannus* and *Corvus*, is very weakly developed. This is especially true of the last two genera in which the proximal portion of the muscle is represented only by a thin tendinous cord. However, a short distance above the lower end of the tarso-metatarsus there is a small and weak fleshy portion. The origin in *Buteo* and *Falco* is limited to about the proximal half of the tarso-metatarsus. The entire muscle is confined to about the distal two-thirds in *Fulica* and *Chaetura;* to the distal two-fifths in *Chordeiles*. In the latter it is very stout.

Burt (1930) does not give the Abd. d. IV for the woodpeckers. It is clearly present, although weakly developed, in all of these birds examined: *Colaptes auratus, Dryobates villosus, Melanerpes erythrocephalus,* and *Sphyrapicus varius*.

Insertion is always on the lateral side of the base of the proximal phalanx of the fourth toe.

A Proposed Revision of Garrod's Myological Formula

Garrod (1874a) proposed a formula for representing the presence and absence of certain variable muscles in the thigh of birds. The components of his formula were represented as follows:

A = *M. piriformis, Pars caudi-femoralis.*
B = *M. piriformis, Pars ilio-femoralis.*
X = *M. semitendinosus.*
Y = *Accessorius semitendinosi.*

The ambiens was also considered but was not designated by a symbol. When the thigh muscle formula is written for a certain group of birds the symbols A, B, X and Y represent the presence of the particular muscles for which they stand. If any one of these muscles is absent this is indicated by omitting the corresponding symbol from the formula. These formulae, which were worked out by Garrod for the various orders of birds, have been extensively quoted in taxonomic works (Gadow—1891, Systematischer Theil; Ridgway—1919).

It is proposed that this formula be amplified as follows:
A = *M. piriformis, Pars caudifemoralis.*
B = *M. piriformis. Pars ilio-femoralis.*

C = *M. ilio-trochantericus medius.*
D = *M. glutaeus medius et minimus.*
X = *M. semitendinosus.*
Y = *Accessorius semitendinosi.*
Am = *M. ambiens.*
V = the *vinculum* connecting the tendon of the flexor perforatus digiti III with that of the flexor perforans et perforatus digiti III (Fig. 74).

It is probable that the P. caud. fem. of the piriformis (A) should never have been used in a myological formula, since it is present in almost all birds, being absent mainly in certain aberrant genera and species. This is shown on Plate XXV of Gadow's work (1891). Similarly the semitendinosus (X) is absent in relatively few groups but it is far more significant than A, being absent in all members of several orders. Nevertheless both of these, and especially X, should be retained in the formula. The reason for retaining A is that it has been very widely quoted in the literature. There are many other muscles of the pelvic extremity which are present in most birds but absent in a few restricted groups. Outstanding examples are: peronaeus longus, peronaeus brevis, plantaris and popliteus. These, however, do not show enough variation to warrant their inclusion in a myological formula.

The following is a synopsis of the groups in which these formula muscles are present and absent (including only the forms examined in the present investigation):

A (piriformis, P. caud. fem.).—

Present			Absent
Gavia	*Colinus*	*Bubo*	*Colymbus*
Sula	*Grus*	*Otus*	
Fregata	*Fulica*	*Chordeiles*	
Ardea	*Totanus*	*Chaetura*	
Chen	*Larus*	*Colaptes*	
Cathartes	*Uria*	*Dryobates*	
Buteo	*Zenaidura*	*Tyrannus*	
Falco	*Coccyzus*	*Corvus*	
Pedioecetes			

B (piriformis, P. il. fem.).—

Present		Absent	
Gavia	*Grus*	*Fregata*	*Otus*
Colymbus	*Fulica*	*Sula*	*Coccyzus*
Chen	*Uria*	*Ardea*	*Chordeiles*
Pedioecetes	*Zenaidura*	*Cathartes*	*Chaetura*
Colinus		*Buteo*	*Colaptes*
		Falco	*Dryobates*
		Totanus	*Tyrannus*
		Larus	*Corvus*
		Bubo	

C (ilio-trochantericus medius).—

Present		Absent	
Gavia	*Zenaidura*	*Fregata*	*Totanus*
Colymbus	*Colaptes*	*Sula*	*Uria*
Cathartes	*Dryobates*	*Ardea*	*Coccyzus*
Pedioecetes	*Tyrannus*	*Chen*	*Chordeiles*
Colinus	*Corvus*	*Buteo*	*Chaetura*
Larus		*Falco*	*Bubo*
		Grus	*Otus*
		Fulica	

D (glutaeus medius et minimus).

Present		Absent	
Gavia	*Colinus*	*Colymbus*	*Colaptes*
Sula	*Grus*	*Zenaidura*	*Dryobates*
Fregata	*Fulica*	*Coccyzus*	*Tyrannus*
Ardea	*Totanus*	*Chordeiles*	*Corvus*
Chen	*Larus*	*Chaetura*	
Cathartes	*Uria*		
Buteo	*Bubo*		
Falco	*Otus*		
Pedioecetes			

X (semitendinosus).

Present			Absent
Gavia	*Colinus*	*Coccyzus*	*Fregata*
Colymbus	*Grus*	*Chordeiles*	*Buteo*
Sula	*Fulica*	*Colaptes*	*Falco*
Ardea	*Totanus*	*Dryobates*	*Chaetura*
Chen	*Larus*	*Tyrannus*	*Bubo*
Cathartes	*Uria*	*Corvus*	*Otus*
Pedioecetes	*Zenaidura*		

Y (accessory semitendinosus).

Present		Absent	
Ardea	*Larus*	*Gavia*	*Falco*
Cathartes	*Zenaidura*	*Colymbus*	*Uria*
Pedioecetes	*Coccyzus*	*Fregata*	*Chaetura*
Colinus	*Chordeiles*	*Sula*	*Dryobates*
Grus	*Colaptes*	*Chen*	*Bubo*
Fulica	*Tyrannus*	*Buteo*	*Otus*
Totanus	*Corvus*		

Am (ambiens).

Present		Absent	
Gavia	*Colinus*	*Colymbus*	*Otus*
Sula	*Grus*	*Ardea*	*Colaptes*
Fregata	*Fulica*	*Chordeiles*	*Dryobates*
Chen	*Totanus*	*Chaetura*	*Tyrannus*
Cathartes	*Larus*	*Bubo*	*Corvus*
Buteo	*Uria*		
Falco	*Zenaidura*		
Pedioecetes	*Coccyzus*		

V (vinculum connecting the tendon of the Flex. per. d. III with that of the F. p. et p. d. III).

Present		Absent	
Gavia	*Grus*	*Colymbus*	*Chaetura*
Sula	*Fulica*	*Fregata*	*Bubo*
Chen	*Totanus*	*Ardea*	*Otus*
Cathartes	*Larus*	*Buteo*	*Colaptes*
Pedioecetes	*Zenaidura*	*Falco*	*Dryobates*
Colinus		*Uria*	*Tyrannus*
		Coccyzus	*Corvus*
		Chordeiles	

The eight components of this muscle formula are found in various combinations in the different taxonomic groups of birds. The combinations encountered, together with the birds showing them, are given below.

ABCDXYAmV.—*Pedioecetes, Colinus*
ABDXYAmV.—*Grus, Fulica*
ABCDXAmV.—*Gavia*
ADXYAmV.—*Totanus*
ADXAmV.—*Sula*
ACXY.—*Colaptes, Tyrannus, Corvus*
ADAm.—*Fregata, Buteo, Falco*
AXY.—*Chordeiles*
AD.—*Bubo, Otus*
A.—*Chaetura*
ABCXYAmV.—*Zenaidura*
ACDXYAmV.—*Cathartes, Larus*
ABDXAmV.—*Chen*
ABDXAm.—*Uria*
AXYAm.—*Coccyzus*
ADXY.—*Ardea, Butorides*
ACX.—*Dryobates*
BCX.—*Colymbus*

It will readily be seen that these combinations may lead to very artificial groupings of very dissimilar birds (Garrod—1874a, p. 114). It would be ridiculous to suppose that *Fregata,* for example, is closely related to the birds of prey simply because it has the same muscle formula. However, such considerations by no means condemn a proper use of myological formulae. These furnish a concise expression of myological peculiarities and, to a limited extent, a measurement of specialization by reduction, assuming that all of these eight characters were present in the primitive ancestral bird. The fact that all are present in the fowls *(Pedioecetes* and *Colinus),* birds that are notoriously generalized, is a strong argument in support of such a view. In any event these formulae can at least serve as aids in characterizing the higher groups of birds.

Gadow (1891, p. 208), in summing up the significance of myological formulae, states in effect that such considerations could be of taxonomic value, although also misleading; they can at least give the first blow to the assumed relationship of doubtful genera, but the majority of cases compel us to attribute no great significance to them.

Myological characters are of taxonomic value only when they are employed with due regard to *all other known morphological facts* (Garrod—1874a, p. 114). In the case already cited of *Fregata* and the birds of prey, it is a simple matter to show by osteological and other means that, although these birds have the same formula (ADAm), they are by no means closely related, but have independently acquired the same formula by reduction. However, it is unnecessary in this case to fall back upon osteological and other characters in order to prove the great dissimilarity between these two groups. An examination of the *entire* musculature of the pelvic limb discloses in many ways a radical disagreement.

It is widely believed—and this is reflected in the current classification—that the woodpeckers and perching birds are very closely related. This viewpoint is supported by an examination of the myology of the pelvic limb. The formulae not only closely agree (ACX and ACXY in the woodpeckers; ACXY in the Passeriformes) but a close study of all the pelvic muscles shows a very striking similarity.

It has long been considered that the owls and the goat-suckers are somewhat closely allied and these groups are placed close together in contemporary avian classification. However, there is nothing in the pelvic myology of these birds to confirm this belief, at least as far as the species examined in this investigation are concerned. Not only are the formulae radically different

(AXY for *Chordeiles* and AD for *Bubo* and *Otus)* but the general musculature of the hind limb is vastly different in the two groups.

The few cases cited above serve to illustrate the possibility of applying myological characters in a study of taxonomic relationships. An enormous amount of work is yet to be done before such comparisons can lead to very definite conclusions.

Garrod (1874a, p. 116) considered the presence or absence of the ambiens muscle so significant that he divided the Class Aves into two subclasses on this basis. Those groups possessing the ambiens were placed in the Subclass Homalogonatae (typically kneed) and those lacking it in the Subclass Anomalogonatae (abnormally kneed). This classification has not been accepted and there is no reason to suppose that the ambiens is any more significant than any one of several variable muscles of the pelvic limb.

A Synopsis of the Outstanding Modifications of the Muscles of the Pelvic Limb in the Various Species of Birds Studied

Order *Gaviiformes* Family *Gaviidae*

Common loon *(Gavia immer)*

Myological Formula: ABCDXAmV.

Absent: Accessory semitendinosus. — Extensor hallucis longus. — Flexor hallucis brevis.

Rudimentary: Extensor proprius digiti III.—Abductor digiti II.

Deep Flexor Tendons: fuse completely. The common tendon gives off three branches below, one to each fore toe—none to the hallux (Fig. 71). This is Gadow's Type IV (1891, p. 195).

Other Important Modifications: the tendon of insertion of the ambiens passes *lateral* to the Il. tib.; Sar. has an isolated insertion directly on the bone on the medial surface of the *Caput tibiae;* biceps inserts about midway the shank; *Semit.* inserts by a long slender tendon; Add. long single, inserting by a short tendon on the medial side of the distal end of the femur; Tib. ant. with a small accessory tendon of insertion; Per. long. not connected below with the Flex. per. d. III; Gas. enormously developed, with two tendons which unite above the tibial cartilage; P. ext. M. gas. arises from the distal half of the femoral shaft; the P. int. two-headed from the proximal half of the tibia, the Semim. inserting between them; insertion of Flex. per. d. II not clearly perforated; origin of the Flex. per. d. IV extends halfway up the femur; F. p. et p. d. II three-headed; Add. d. II originates from the perforated process and just below it, tendon very long; all of the toe flexors pass through the perforated process in a large common canal.

Order *Colymbiformes* Family *Colymbidae*

Eared grebe *(Colymbus nigricollis californicus)*

Myological Formula: BCX.

Absent: Glutaeus medius et minimus. — Ambiens. — Piriformis, P. caud.

fem. — Accessory semitendinosus. — Semimembranosus. — Peronaeus brevis. — Flexor perforatus digiti II. — Extensor hallucis longus.

Rudimentary: Extensor proprius digiti III. — Extensor brevis digiti IV. — Abductor digiti II.

Deep Flexor Tendons: these fuse and the common tendon trifurcates below, no branch going to the hallux. Gadow's Type IV (1891, p. 195).

Other Important Modifications: the Sar. has an isolated insertion directly on the bone on the medial side of the *Caput tibiae* as in *Gavia;* Il. tib. with two heads of origin; biceps completely concealed by the Il. tib.; Add. long. consists of a P. ext. and P. int.; Tib. ant. with a small accessory tendon of insertion; Per. long. inserts only on the tibial cartilage; Gas. with two tendons which unite above the tibial tartilage; P. int. M. gas. two-headed, arising from a long line down the proximal half of the tibia as in *Gavia;* Add. d. II arises just below the perforated process, the tendon very long; F. p. et p. d. II, F. hal. l., and F. dig. l. pass through the perforated process.

Order *Pelecaniformes* Suborder *Pelecani* Family *Sulidae*
Brewster's booby *(Sula brewsteri)*

Myological Formula: ADXAmV.

Absent: Only one ilio-trochantericus muscle present. — Piriformis, P. il. fem. — Accessory semitendinosus. — Peronaeus brevis.

Rudimentary: Extensor proprius digiti III.

Deep Flexor Tendons: simple vinculum—Gadow's Type I (1891, p. 195).

Other Important Modifications: P. caud. fem. of piriformis with a long narrow tendon of insertion; Semim. and Semit; insert in common; Add. long. consists of a P. ext. and P. int.; Tib. ant. without an accessory tendon of insertion; Per. long. arises from the lateral tibial crest and a long line down the fibular shaft; Gas. with a single tendon; Flex. per. d. III one-headed; the tendon of the F. hal. l. perforates that of the F. hal. brev.; popliteus narrow and weak; Ext. hal l. arises from most of the length of the tarso-metatarsus, the insertion mostly on the base of the proximal phalanx; F. hal. brev. arises from most of the length of the tarso-metatarsus; Add. d. II with origin from most of the length of the tarso-metatarsus, the tendon very short; only the F. dig. l. and the F. hal. l. pass through the perforated process.

Order *Pelecaniformes* Suborder *Fregatae* Family *Fregatidae*
Man-o'-war-bird *(Fregata magnificens)*

Myological Formula: ADAm.

Absent: Ilio-trochantericus medius. — Piriformis, P. il. fem. — Semitendinosus. — Accessory semitendinosus. — Extensor proprius digiti III.

Rudimentary: Ilio-tibialis.

Deep Flexor Tendons: fuse completely. Four tendons given off below. Gadow's Type V (1891, p. 195).

Other Important Modifications: Fem. tib. int. with the tendon of insertion

bifurcated; P. ext. of Add. long. small; the accessory tendon of insertion of the Tib. ant. forms one of the heads of origin of the Ext. brev. d. IV; Per. long. arises from the lateral tibial crest and the shaft of the fibula; Per. brev. very short and giving off an extra tendon which fuses with the tendon of the Per. long.; proximal portion of Gas. tendon single; distal portion of Gas. tendon bifurcated; the Flex. per d. II sends a branch to the base of the hallux; Flex. per. d. III one-headed; at the heel joint the tendon of the F. hal. l. lies directly behind that of the F. dig. l.; the main flexor of the hallux perforates the tendon of the F. hal. brev.; Ext. hal. l. arises from most of the length of the tarso-metatarsus, inserting mostly on the base of the proximal phalanx; Ext. brev. d. IV two-headed; perforated process absent, the two deep flexors simply passing through incompletely ossified grooves.

Order *Ciconiiformes* Suborder *Ardeae* Family *Ardeidae*
Great blue heron *(Ardea herodias)*

Myological Formula: ADXY.

Absent: Ilio-trochantericus medius. — Ambiens. — Piriformis, P. il. fem.

Rudimentary: None.

Deep Flexor Tendons: vinculum simple and very feebly developed. Type I of Gadow (1891, p. 195).

Other Important Modifications: Fem. tib. ext. independently developed, arising from the distal half of the femur; Add. long. consists of a P. ext. and P. int.; Tib. ant. with a small accessory tendon of insertion; Gas. with a single tendon; Flex. per. d. III one-headed; Flex. per. d. IV two-headed, also attached to fibular shaft; origin of the F. p. et p. d. III connected with fibular shaft; tendon of the F. hal. l. perforates that of the F. hal. brev.; Ext. hal. l. fleshy all the way to the base of hallux; Abd. dig. II not connected with Met. I; tendon of the F. hal. brev. double for a short distance; Add. d. II confined to distal half of tarso-metatarsus; lumbricalis well developed and fleshy; fleshy portions of shank muscles limited mainly to the proximal half of the tibio-tarsus, the tendons very long; no perforated process but the F. dig. l. and the F. hal. l. pass through incompletely ossified bony grooves.

Order *Anseriformes* Suborder *Anseres* Family *Anatidae*
Lesser snow goose *(Chen hyperborea)*

Myological Formula: ABDXAmV.

Absent: Ilio-trochantericus medius. — Accessory semitendinosus.

Rudimentary: Flexor hallucis brevis. — Lumbricalis.

Deep Flexor Tendons: the two tendons fuse but at the point of fusion the F. hal. l. sends a weak branch to the hallux. Type II (Gadow—1891, p. 195).

Other Important Modifications: ambiens with a broad origin from the pubis; Semim. arises from the midventral portion of the ischium; Bic. fem. arises from about the anterior half of the post-acetabular ilium; Isch. fem.

arises from about the anterior half of the ischium; Add. long. consists of a P. ext. and P. int.; Tib. ant. with a small accessory tendon of insertion; Gas. with two separate tendons which fuse above the tibial cartilage; P. med. M. gas. forms a slender tendon which fuses below with the P. int.; P. int. M. gas. extends around the front of the knee; insertion of the Flex. per. d. II not perforated at all; Flex. per. d. III two-headed; F. p. et p. d. III not connected with shaft of fibula; tendon of F. hal. l. does not perforate that of the F. hal. brev.; popliteus diagonal and narrow; Ext. hal. l. very weak and confined to the distal half of the tarso-metatarsus; Ext. pro. d. III limited to the distal fourth of the tarso-metatarsus. Perforated process: only the F. dig. l. passes through a bony canal.

Order *Falconiformes* Suborder *Cathartae*

Family *Cathartidae:* Turkey vulture *(Cathartes aura septentrionalis)*

Myological Formula: ACDXYAmV.

Absent: Piriformis, P. il. fem.

Rudimentary: Extensor proprius digiti III. — Lumbricalis.

Deep Flexor Tendons: the two unite firmly and there is no vinculum. The common tendon gives off four branches below, the smallest to the hallux, the largest to the medius digit. Type V (Gadow—1891, p. 195).

Other Important Modifications: Il. tib. with post-acetabular portion well developed, overlapping most of the Bic. fem.; Add. long. consists of a P. ext. and P. int.; Semit. arises mainly from the ischium; Tib. ant. without an accessory tendon of insertion; Per. long. very wide, arising from the entire anterior tibial crest and a long line down the lateral side of the fibula; Gas. with an undivided tendon of insertion; P. int. M. gas. extends around the front of knee; Plantaris typical, with a long slender tendon; insertion of the Flex. per. d. II not perforated at all; Flex. per d. III arises from the *Regio intercondyloidea* in common with the Flex. per. d. IV; tendon of Flex. per. d. IV trifurcated, inserting mainly on the bases of phalanges II, III, and IV; belly of F. dig. l. typical, not visible superficially on the lateral side of the shank; belly of the F. hal. l. lies anterior to the common head of origin of the Flex. per. d. III and IV; Ext. hal. l. one-headed, fleshy all the way to base of hallux; Abd. dig. II confined to the distal third of the tarso-metatarsus, arising from Met. I and II; F. hal. brev. arises from almost the entire length of the tarso-metatarsus, tendon undivided but clearly perforated by the F. hal. l.; no perforated process.

Order *Falconiformes* Suborder *Falcones*

Family *Accipitriidae:* *Mississippi kite *(Ictinia misisippiensis)*.
Cooper's hawk *(Accipiter cooperi)*.
Red-tailed hawk *(Buteo borealis)*.
Swainson's hawk *(Buteo swainsoni)*.
Marsh hawk *(Circus hudsonius)*.

* The part of the leg below the intertarsal joint not available since the specimen was used for a study skin.

Family *Falconidae:* *Prairie falcon *(Falco mexicanus).*
Duck hawk *(Falco peregrinus anatum).*
Sparrow hawk *(Falco sparverius).*

Myological Formula: ADAm.

Absent: Ilio-trochantericus medius. — Piriformis, P. il. fem. — Semitendinosus. — Accessory semitendinosus. — Plantaris absent in Accipitriidae, present in *Falco.*

Rudimentary: Extensor proprius digiti III in *Falco* (well developed in Accipitriidae). — Lumbricalis.

Deep Flexor Tendons: in addition to the extensive vinculum there is also a heavy tendinous connection between the lower end of the tendon of the F. hal. l. and the branch from the main flexor tendon passing to the index digit. Type III (Gadow—1891, p. 195).

Other Important Modifications: Il. tib. not connected with the post-acetabular ilium, also does not overlap the Bic. fem.; Add. long. consists of a P. ext. and P. int.; Tib. ant. connected to tibial shaft for a long distance, also has an accessory tendon of insertion; Per. long. arises from a long line down the lateral side of the fibular shaft; insertion of the Flex. per. d. II not perforated at all; Flex. per. d. III two-headed; tendon of F. hal. l. lies directly behind that of the F. dig. l. at the heel joint; F. hal. l. two-headed, one from the shaft of the femur just above the condyles, the other from the *Regio intercondyloidea;* Ext. hal. l. two-headed; tendon of insertion of F. hal. brev. not perforated by that of the F. hal. l.; Add. d. II weak, with a long tendon of insertion; origin of the Abd. d. IV restricted to the proximal half of the tarso-metatarsus. Perforated process: none—no tendons pass through bony canals.

In addition to the common characters given above the Accipitriidae and *Falco* differ in several features. These are listed below.

Ambiens.—The tendon of insertion in the Accipitriidae passes medially to the tendon of the Bic. fem. In *Falco* it passes laterally to this tendon. This latter condition was observed in no other bird.

Femori-tibialis internus.—Reaching farther proximally than the insertion of the iliacus in the Accipitriidae; much shorter in *Falco.*

Semimembranosus.—Typical in the Accipitriidae; double in *Falco.*

Gastrocnemius.—In the Accipitriidae the proximal end of the tendon of insertion is double, the two tendons uniting above the tibial cartilage. The tendon is undivided in *Falco.*

Plantaris.—Absent in the Accipitriidae. Powerfully developed in *Falco.*

Flexor perforatus digiti III.—Arises in common with the posterior head of the Flex. per. d. IV in the Accipitriidae. Arises in *Falco* by a long independent tendon.

Flexor perforatus digiti IV.—In the Accipitriidae the posterior head arises from the *Regio intercondyloidea* in common with the preceding muscle. In *Falco* this head is lacking.

Flexor perforans et perforatus digiti III.—Arises in the Accipitriidae only from the tibial crest and the adjacent patellar tendon. In *Falco* it arises in addition from a long line down the shaft of the fibula.

Flexor digitorum longus.—Powerfully developed in the Accipitriidae, much of the belly being visible superficially on the lateral side of the shank. In *Falco* the muscle is typical—much smaller and no part visible superficially.

Extensor hallucis longus.—In the Accipitriidae the medial head forms a fleshy sheath about the tendon of the Ext. dig. l. This is not the case in *Falco.*

Extensor proprius digiti III.—Confined to the distal half or third of the tarso-metatarsus in the Accipitriidae. Rudimentary in *Falco,* limited to about the distal eighth of the tarso-metatarsus.

Abductor digiti II.—Extends almost the entire length of the tarso-metatarsus in the Accipitriidae and has no connection with Met. I. Limited to about the distal fourth of the tarso-metatarsus in *Falco* and arising almost wholly from the first metatarsal bone.

Flexor hallucis brevis.—The tendon of insertion is distinctly double in the Accipitriidae, especially at the lower end; in *Falco* the tendon is undivided.

Order *Galliformes* Suborder *Galli*

Family *Tetraonidae:* Sharp-tailed grouse *(Pedioecetes phasianellus).*
Family *Perdicidae:* Bob-white *(Colinus virginianus).*

Myological Formula: ABCDXYAmV.

Absent: Adductor digiti II in *Pedioecetes,* present in *Colinus.*

Rudimentary: none.

Deep Flexor Tendons: connected by a simple vinculum. Type I (Gadow —1891, p. 195).

Other Important Modifications: Add. long. consists of a P. ext. and P. int.; no accessory tendon of insertion to the Tib. ant.; P. int. M. gas. extends around the front of the knee; tendon of Gas. single; Flex. per. d. III two-headed, the two forming separate tendons which unite above the tibial cartilage; Flex. per. d. IV two-headed, the biceps tendon passing between them; F. p. et p. d. III not connected with shaft of fibula; the tendon of F. hal. l. perforates that of the F. hal. brev.; Ext. hal. l. arises from most of the length of the tarso-metatarsus; Ext. pro. d. III limited to the distal third of the tarso-metatarsus. Perforated process: only three tendons pass through bony canals. In *Pedioecetes* these are the F. p. et p. d. II, F. hal. l., and F. dig. l. In *Colinus* these are the Flex. per. d. II, F. p. et p. d. II, and F. dig. l.

Pedioecetes and *Colinus* differ in the following respects:

Obturator internus.—Typical in *Pedioecetes;* in *Colinus* it arises as usual and also from the ventral surface of the latero-posterior portion of the ilium. *Phasianus colchicus torquatus* agrees with *Colinus*.

Flexor digitorum longus.— In *Pedioecetes* connected with the anterior tibial crest; typical in *Colinus*.

Adductor digiti II.—Absent in *Pedioecetes;* present in *Colinus* (and *Phasianus colchicus torquatus)*.

In *Pedioecetes* the bellies of many of the shank muscles contain longitudinal splinters of bone. There are none in *Colinus*.

Order *Gruiformes* Suborder *Grues*

Family *Gruidae:* Little brown crane *(Grus canadensis)*.
Family *Rallidae:* American coot *(Fulica americana)*.

Myological Formula: ABDXYAmV.

Absent: Ilio-trochantericus medius.

Rudimentary: Extensor proprius digiti III.

Deep Flexor Tendons: connected by a simple vinculum. Type I (Gadow —1891, p. 195).

Other Important Modifications: Fem. tib. ext. independently developed; Semit. has no connection with the caudal vertebrae; Add. long. consists of a P. ext. and P. int.; P. int. M. gas. runs around the front of the knee; Flex. per. d. IV two-headed, the biceps tendon passing between them; F. p. et p. d. III not connected with the shaft of fibula; F. hal. l. does not perforate the tendon of the F. hal. brev.; Ext. hal. l. arises from most of the length of the tarso-metatarsus, insertion mainly on the base of the proximal phalanx; many of the shank muscles have longitudinal splinters of bone running through the bellies; perforated process poorly developed, only the F. dig. l. passing through a bony canal in *Grus*, the F. dig. l. and Flex. per. d. II in *Fulica*.

Grus and *Fulica* differ as follows:

Ambiens.—Typical in *Grus;* the belly partly double in *Fulica* (also in *Porzana carolina)*.

Obturator internus.—Typical in *Grus;* in *Fulica* double, with the lateral head arising from the ventral surface of the postero-lateral portion of the ilium. *Porzana carolina* agrees with *Fulica*.

Tibialis anterior.—A small accessory tendon of insertion in *Fulica* but not in *Grus*.

Gastrocnemius.—Tendon of insertion single in *Grus*, two independent tendons in *Fulica*—these fuse above the tibial cartilage.

Flexor perforatus digiti III.—In *Grus* the two bellies fuse and only one tendon is formed. In *Fulica* the bellies form separate tendons which fuse below.

Order *Charadriiformes* Suborder *Charadrii*
Family *Scolopacidae:* Greater yellowlegs *(Totanus melanoleucus).*
Lesser yellowlegs *(Totanus flavipes).*

Myological Formula: ADXYAmV.

Absent: Ilio-trochantericus medius. — Piriformis, P. il. fem.

Rudimentary: Extensor proprius digiti III.

Deep Flexor Tendons: connected by a simple vinculum. Type I (Gadow —1891, p. 195).

Other Important Modifications: Fem. tib. ext. independently developed; Add. long. consists of a P. ext. and P. int.; Tib. ant. with a small accessory tendon of insertion; P. int. M. gas. extends around the front of the knee; Gas. with two tendons which unite above the tibial cartilage; the two heads of the Flex. per. d. III unite, forming only one tendon; Flex. per. d. IV two-headed, the biceps tendon passing between them; F. p. et p. d. III not connected with the shaft of fibula; Ext. hal. l. confined to the distal half of the tarso-metatarsus; F. hal. brev. with the tendon of insertion double distally, not perforated by F. hal. l.; Add. d. II arises just below the perforated process, the tendon being very long; only the F. dig. l. passes through the perforated process; fleshy portion of shank muscles confined to the proximal half of the tibio-tarsus, tendons very long.

Order *Charadriiformes* Suborder *Lari* Family *Laridae*
Franklin's gull *(Larus pipixcan).*

Myological Formula: ACDXYAmV.

Absent: Piriformis, P. il. fem.

Rudimentary: Extensor proprius digiti III.

Deep Flexor Tendons: the two tendons fuse and the common tendon trifurcates below, no branch going to the hallux. Type IV (Gadow—1891, p. 195).

Other Important Modifications: Fem. tib. ext. independently developed; Add. long. shows only very faint indications of a division into a P. ext. and P. int.; Tib. ant. without an accessory tendon of insertion; belly of the Per. long. not superficial but covered by other muscles, the origin connected with the shaft of the tibia and fibula; P. med. M. gas. arises by a long slender tendon; P. int. M. gas. extends around the front of the knee; the Gas. forms two distinct tendons which unite above the tibial cartilage; the two heads of the Flex. per. d. III unite, forming only one tendon; Flex. per. d. IV two-headed, the biceps tendon passing between them; F. p. et p. d. II arises from the entire anterior crest of the tibia; F. p. et p. d. III not connected with the shaft of the fibula; popliteus narrow and weak; Ext. hal. l. arises by two heads, inserts mainly on the proximal phalanx; F. hal. brev. with the tendon double at the lower end and not perforated by the tendon of the F. hal. l.; Abd. dig. II not connected with Met. I; Add. d. II arising just below the perforated process, tendon long and slender; fleshy portions of the shank muscles confined mainly to the proximal half of the tibio-tarsus, the tendons very long: only the F. dig. l. passes through the perforated process.

Order *Charadriiformes* Suborder *Alcae* Family *Alcidae*
California murre *(Uria aalge californica)*

Myological Formula: ABDXAm.

Absent: Ilio-trochantericus medius. — Accessory semitendinosus. — Extensor hallucis longus. — Flexor hallucis brevis.

Rudimentary: Ambiens. — Extensor proprius digiti III.

Deep Flexor Tendons: the two tendons fuse and the common tendon trifurcates below. Hallux absent. Type IV (Gadow—1891, p. 195).

Other Important Modifications: the minute ambiens tendon does not pass the knee joint; Add. long. undivided; Tib.ant. without an accessory tendon of insertion; Per. long. connected with the shaft of the fibula; P. int. M. gas. double, the Semim. inserting between the two heads; P. int. M. gas. extends around the front of the knee; Gas. with two distinct tendons which unite above the tibial cartilage; Flex. per. d. II arises from the shaft of the fibula, the tendon of insertion not perforated; the two heads of the Flex. per. d. III form separate tendons which fuse above the tibial cartilage; Flex. per. d. IV one-headed and attached to the shaft of the fibula; F. p. et p. d. III attached to a long line down the fibular shaft; Abd. dig. II extends halfway up the tarso-metatarsus; Add. d. II arises just below the perforated process, tendon long; the two deep flexors pass through incompletely ossified grooves but there is no perforated process.

Order *Columbiformes* Suborder *Columbae* Family *Columbidae*
Mourning dove *(Zenaidura macroura)*

Myological Formula: ABCXYAmV.

Absent: Glutaeus medius et minimus.

Rudimentary: none.

Deep Flexor Tendons: connected by a simple vinculum. Type I (Gadow —1891, p. 195).

Other Important Modifications: Fem. tib. ext. independently developed; the P. caud. fem. of the piriformis arises thick and mostly fleshy from the coccyx; Add. long. a single undivided sheet; Tib. ant. without an accessory tendon of insertion; Per. long. attached to a long line down the shaft of the fibula; Per. brev. short, limited to the distal half of the tibio-tarsus; Gas. with a single tendon; the two branches to the tendon of insertion of the Flex. per. d. IV are separately perforated; F. p. et p. d. III attached to a long line down the fibular shaft, the two branches to the tendon of insertion separately perforated; tendon of the F. hal. l. perforates that of the F. hal. brev.; Ext. hal. l. double, the two parts inserting separately; Ext. pro. d. III confined to the distal two-thirds of the tarso-metatarsus; F. hal. brev. arises from most of the length of the tarso-metatarsus; Abd. dig. II reaches halfway up the tarso-metatarsus, not connected with Met. I; Add. d. II arises from most of the length of the tarso-metatarsus; lumbricalis unusually large and muscular. The

perforated process is fairly well developed, the following tendons passing through bony canals: F. dig. l., F. hal. l., Flex. per. d. II, and F. p. et p. d. II.

Order *Cuculiformes* Suborder *Cuculi* Family *Cuculidae*
Yellow-billed cuckoo *(Coccyzus americanus)*

Myological Formula: AXYAm.

Absent: Ilio-trochantericus medius. — Glutaeus medius et minimus. — Piriformis, P. il. fem.

Rudimentary: none.

Deep Flexor Tendons: connected by a simple vinculum. Type I (Gadow —1891, p. 195).

Other Important Modifications: the middle portion of the Il. tib. is not fleshy at any point; Add. long. consists of a P. ext. and a P. int.; Tib. ant. with a small accessory tendon of insertion; Per. long. very narrow, the origin attached to a long line down the shaft of the tibia and fibula; Gas. with a single tendon; belly of the plantaris very long, reaching two-thirds the way down the shank; Flex. per. d. II inserts on the distal portion of the proximal phalanx; the femoral head of the Flex. per. d. III arises by a long slender tendon; F. p. et p. d. III attached to the shaft of the fibula for a short distance; the tendon of the F. hal. l. perforates that of the F. hal. brev.; Ext. pro. d. III arises from most of the length of the tarso-metatarsus; the Ext. brev. d. IV is very powerful and the tendon does not pass through a canal; Abd. dig. II reaches half-way up the tarso-metatarsus; Add. d. II arises just below the perforated process, the tendon very long; lumbricalis unusually large and muscular; origin of the Abd. d. IV reaches up on the tibial cartilage; only the F. dig. l. and the F. hal. l. pass through the perforated process.

Order *Strigiformes* Family *Strigidae*
Screech owl *(Otus asio)*
Great horned owl *(Bubo virginianus)*

Myological Formula: AD.

Absent: Ilio-trochantericus medius. — Ambiens. — Piriformis, P. il. fem. — Semitendinosus. — Accessory semitendinosus. — Peronaeus longus. — Plantaris.

Rudimentary: Lumbricalis.

Deep Flexor Tendons: connected by a simple but extensive vinculum. Type I (Gadow—1891, p. 195).

Other Important Modifications: sartorius arises entirely from the ventral border of the ilium; Il. tib. not connected with the post-acetabular ilium; Add. long. consists of a P. ext. and P. int.; Tib. ant. with two large tendons of insertion; Ext. dig. l. attached to the anterior surface of the fibula; the origin of the Per. brev. extends onto the anterior surface of the tibia at the distal end; Gas. with a single tendon; P. int. M. gas. reaches up onto the internal condyle of the femur; Flex. per. d. II two-headed, the tendon of the Bic. fem. passing between them; the two heads of the Flex. per. d. III unite and only

one tendon is formed; the biceps tendon passes between the two heads of the Flex. per. d. IV; F. p. et p. d. III connected neither with the tibia nor the shaft of the fibula; F. dig. l. extremely powerful and the belly visible superficially for the entire length of the shank on both the outer and inner sides; F. dig. l. arises by three heads; F. hal. l. two-headed, the main head from the *Regio intercondyloidea,* the small head from the posterior side of the joint capsule of the knee; Ext. hal. l. two-headed, the main one from the internal malleolus of the tibio-tarsus, the small one from the proximal end of the tarso-metatarsus; Ext. pro. d. III arises from almost the entire length of the tarso-metatarsus; F. hal. brev. with two tendons which insert separately, not perforated by the F. hal. l.; Add. d. II arises from about the proximal third of the tarso-metatarsus, the tendon very long; the bellies of many of the shank muscles contain longitudinal splinters of bone; perforated process absent, no tendons passing through bony canals.

Bubo and *Otus* were found to differ in the following ways:

Flexor digitorum longus.—In *Bubo* the tendon trifurcates as usual near the lower end of the tarso-metatarsus. In *Otus* it divides into two branches near the proximal end of the tarso-metatarsus, the inner supplying digits II and III, the outer digit IV.

Extensor proprius digiti III.—The proximal end of the origin in *Bubo* lies lateral to the tendon of the Tib. ant.; in *Otus* the belly is divided by the Tib. ant. insertion.

Order *Caprimulgiformes* Suborder *Caprimulgi*
Family *Caprimulgidae:* Nighthawk *(Chordeiles minor)*

Myological Formula: AXY.

Absent: Ilio-trochantericus medius. — Glutaeus medius et minimus. — Ambiens. — Piriformis, P. il. fem. — Peronaeus brevis.

Rudimentary: none.

Deep Flexor Tendons: the two tendons fuse and the common tendon divides below into four branches. Type V (Gadow—1891, p. 195).

Other Important Modifications: iliacus very strongly developed; only the posterior portion of the Il. tib. is fleshy; Add. long. consists of a P. ext. and P. int.; Tib. ant. with a small accessory tendon of insertion; Gas. with a single tendon; the two heads of the Flex. per. d. III fuse and only one tendon is formed; F. p. et p. d. III not connected with the fibular shaft, the two branches to the tendon of insertion separately perforated; popliteus diagonal and narrow; Ext. hal. l. fleshy all the way to the base of the hallux; F. hal. brev. fleshy all the way to the base of the hallux, tendon not perforated by the main flexor tendon; Ext. pro. d. III extends halfway up the tarso-metatarsus; Abd. dig. II not connected with Met. I; Add. d. II arises from almost the entire length of the tarso-metatarsus, the tendon very short; lumbricalis unusually strong and well developed; Abd. d. IV short, limited to the distal two-fifths of the tarso-metatarsus; only the F. dig. l. passes through the perforated process.

In spite of the fact that the nighthawk has notoriously small and weak feet, the intrinsic muscles of the foot are unusually strong and stout.

Order *Micropodiiformes* Suborder *Micropodii*
Family *Micropodidae* Chimney Swift *(Chaetura pelagica)*

Myological Formula: A.

Absent: Ilio-trochantericus medius. — Glutaeus medius et minimus. — Ambiens. — Piriformis, P. il. fem. — Semitendinosus. — Accessory semitendinosus. — Peronaeus longus. — Plantaris. — Flexor perforatus digiti II. — Popliteus.

Rudimentary: Extensor proprius digiti III.

Deep Flexor Tendons: fuse completely. Four tendons given off below. Gadow's Type V (1891, p. 195).

Other Important Modifications: Post-acetabular portion of Il. tib. absent; P. caud. fem. of piriformis inserts about midway the thigh by a long slender tendon; Bic. fem. superficial, not covered by the Il. tib.; Add. long. single, arising from the ventral edge of the pubis only; Tib. ant. without an accessory tendon of insertion; the three branches of the tendon of the Ext. dig. l. are undivided and insert only on the unguinal phalanges; Gas. with two tendons which unite above the tibial cartilage; P. int. M. gas. double, the Semim. inserting between the two heads; Flex. per. d. III and Flex. per. d. IV one-headed, arising together from the external condyle and a small portion of the fibular shaft; insertion of the Flex. per. d. IV undivided; F. p. et p. d. III arises only from the lateral surface of the fibula; tendon of F. hal. l. does not perforate that of the F. hal. brev.; tendon of the F. hal. l. lies directly behind that of the F. dig. l. at the tibial cartilage; no perforated process, the two deep flexor tendons simply passing through incompletely ossified grooves in the bone.

Order *Piciformes* Suborder *Pici* Family *Picidae*
Flicker *(Colaptes auratus)*
Hairy woodpecker *(Dryobates villosus)*

Myological Formulae: ACXY *(Colaptes)*
ACX *(Dryobates)*

Absent: Glutaeus medius et minimus. — Ambiens. — Accessory semitendinosus (in *Dryobates;* present in *Colaptes).* — Popliteus. — Extensor brevis digiti IV. — Abductor digiti II. — Adductor digiti II.

Rudimentary: Abductor digiti IV.

Deep Flexor Tendons: very peculiar. The two tendons are connected by a simple vinculum, but the F. dig. l. supplies only the third toe, the F. hal. l. trifurcating to supply digits I, II and IV. Type VI (Gadow—1891, p. 195).

Other Important Modifications: the middle portion of the Il. tib. is tendinous throughout its entire length; the tibial insertion of the Semit. is entirely proximal to the insertion of the Semim.; Add. long. with very little

indication of a division into two parts; Tib. ant. without an accessory tendon of insertion; the branches of the Ext. dig. l. passing to digits II and IV insert only on the unguinal phalanges; Per long. inserts only on the tibial cartilage and has no connection with the Flex. per. d. III; Gas. with a single tendon; the F. p. et p. d. III passes through the tibial cartilage in a separate canal; Flex. per. d. III and Flex. per. d. IV pass through the tibial cartilage in the same canal, the two firmly bound together in a sheath; Flex. per. d. IV two-headed, the main head from the *Regio intercondyloidea*, the small head from the external condyle and *Caput fibulae;* Flex. per. d. IV inserts by two branches, neither of which is perforated; the tendon of insertion of the F. p. et p. d. II is not perforated at all; F. p. et p. d. III connected with a long line down the fibular shaft, the two branches of the tendon of insertion separately perforated; F. hal. l. two-headed, one from the *Regio intercondyloidea*, the other from the *Caput fibulae* and much of the fibular shaft; Ext. pro. d. III reaches up almost to the Tib. ant. insertion; the tendon of the F. hal. brev. perforated by that of the F. hal. l.; perforated process complete, all of the long flexor tendons passing through bony canals.

Colaptes and *Dryobates* were found to differ as follows:

Piriformis.—Insertion tendinous in *Colaptes,* fleshy in *Dryobates.*

Semitendinosus.—Typical in *Colaptes,* the accesorius absent in *Dryobates.*

Flexor perforatus digiti III.—The two heads in *Colaptes* form separate tendons which unite above the tibial cartilage; in *Dryobates* the bellies unite and only one tendon is formed.

Order *Passeriformes* Suborder *Tyranni* Family *Tyrannidae*
Eastern kingbird *(Tyrannus tyrannus)*

Order *Passeriformes* Suborder *Passeres* Family *Corvidae*
Eastern crow *(Corvus brachyrhynchos)*
American raven *(Corvus corax sinuatus)*

Myological Formula: ACXY.

Absent: Glutaeus medius et minimus. — Ambiens. — Piriformis, P. il. fem. — Popliteus. — Extensor proprius digiti III. — Extensor brevis digiti IV. — Abductor digiti II. — Adductor digiti II.

Rudimentary: Flexor hallucis brevis, especially in *Corvus.* — Abductor digiti IV.

Deep Flexor Tendons: there is no connection between the two tendons. Type VII (Gadow—1891, p. 195).

Other Important Modifications: the Obt. ext. consists of two distinct heads; Add. long. divided into a P. ant. and P. post.; Tib. ant, without an accessory tendon of insertion; Gas. with a single tendon; Flex. per. d. II with most of the belly visible superficially on the lateral side of the shank, the origin from the external condyle; tendons of the Flex. per. d. III and Flex. per. d. IV pass through the same canal in the tibial cartilage, the F. p. et p. d. III passing through a different canal; Flex. per. d. III one-headed; F. p. et

p. d. III connected with a long line down the fibular shaft; F. dig. l. with two heads, one from the posterior side of the external condyle and the main head from the posterior surfaces of the tibia and fibula; F. hal. l. two-headed, a small head from the external condyle and the main head from the *Regio intercondyloidea,* the biceps tendon passing between them; tendon of the F. hal. brev. perforated by that of the F. hal l.; perforated process complete, all of the long flexor tendons passing through the bony canals.

The various species of Passeriformes examined were found to differ only in the following important respect:

Ilio-tibialis.—In the Tyrannidae and Hirundinidae the post-acetabular portion is absent, the entire belly of the Bic. fem. consequently being visible superficially on the lateral side of the thigh. In the representatives of the twenty other families of Passeriformes examined for this character the muscle has the usual development.

Summary and Conclusion

Representatives of sixteen of the twenty North American orders of birds were studied from a comparative viewpoint, to determine myological peculiarities of possible taxonomic value. All of the muscles of the pelvic limb were examined in thirty-two species. In addition numerous other species were studied in order to ascertain certain specific points. Examination was mainly by gross dissection but celloidin cross sections were prepared for five species at various levels on the hind limb. This latter method has apparently not been used before in studies on the appendicular muscles of birds. The nomenclature of Gadow (Bronn's Thier-Reichs) is used, but this is revised to conform as closely as possible with the BNA.

Colymbus is far more specialized than *Gavia.* In the former eight muscles of the hind limb are absent, in the latter only three. Nevertheless, they agree in several striking peculiarities.

Sula and *Fregata,* the two representatives of the Order Pelecaniformes studied, differ greatly in the musculature of the pelvic limb.

Gadow (1891, p. 182) states that the peronaeus brevis is absent in *Ardea;* however, it is well developed in *Ardea herodias.*

The hawks differ from the falcons in several important respects. *Cathartes* is radically different from the hawks and falcons and shows a far more primitive pelvic musculature. The myological formula for *Cathartes* is ACDXY-AmV; for the hawks and falcons, ADAm.

Although *Fregata* and the birds of prey have the same myological formula (ADAm) they differ profoundly in numerous other features of the musculature of the pelvic appendage.

The semimembranosus muscle is double in *Falco,* but in no other bird examined.

Gadow (1891, p. 186) states that the plantaris muscle is lacking in all the birds of prey. However in the several species of *Falco* studied this muscle is not only present but is more powerfully developed than in any other

bird examined, the belly reaching almost to the tibial cartilage. A typical plantaris is present in *Cathartes*.

A rudimentary but very definite ambiens muscle is present in *Uria aalge californica*, although all members of the Alcidae are generally stated to lack this muscle. Gadow (1891, Plate XXV) recorded the ambiens for *Uria* but this apparently has escaped the notice of taxonomists.

The extensor hallucis longus is double in *Zenaidura* and *Columba livia*, with two separate points of insertion. *Larus* and *Sterna* show a tendency in this direction.

A study of the musculature of the pelvic limb in a goat-sucker *(Chordeiles)* and in certain owls *(Bubo* and *Otus)*, fails to disclose any unusual similarity. The formulae are very different (AXY for *Chordeiles* and AD for the owls) and there are numerous other striking differences in the pelvic musculature.

All of the species of the Tyrannidae and Hirundinidae studied differ from representatives of the twenty other families of Passeriformes examined in the absence of the post-acetabular portion of the ilio-tibialis muscle. It is possible that this character may prove to be of significance in the classification of the order.

It is proposed that Garrod's myological formula (A-B, X-Y and ambiens) be amplified to include the ilio-trochantericus medius, the glutaeus medius et minimus, and the vinculum connecting the tendon of the flexor perforatus digiti III with that of the flexor perforans et perforatus digiti III. These three structures are designated in the formula by the letters C, D, and V, respectively. There are several other muscles of the pelvic limb that are present in most birds but absent in a few restricted groups. These, however, do not show enough variation to warrant their inclusion in a myological formula. Outstanding examples are: peronaeus longus, peronaeus brevis, plantaris and popliteus.

All of the muscles known to occur in the hind limb of birds are present in representatives of the Order Galliformes, indicating a generalized condition. From one to nine muscles (or parts of muscles) are absent in representatives of the other orders examined. Only one is lacking in *Cathartes* and *Zenaidura*. The greatest reduction in number was found in *Colymbus* (8), *Chaetura* (9), *Dryobates* (7), and the Passeriformes (8).

In many birds there are small fibro-elastic ligaments passing from the upper surfaces of the penultimate phalanges of the toes to the unguinal phalanges. These function as automatic extensors of the claws.

The flexor perforatus digiti II was found to be absent only in *Colymbus nigricollis californicus* and *Chaetura pelagica*. The four other perforated flexor muscles were present in all cases.

In *Fulica americana, Porzana carolina, Colinus virginianus* and *Phasianus colchicus torquatus*, the obturator internus is peculiar in arising in part from the ventral surface of the postero-lateral portion of the ilium. The muscle is double in *F. americana* and *P. carolina*.

The tibialis anterior in many birds gives off, below, a small accessory tendon of insertion.

In some birds the tendons of insertion of certain perforated flexor muscles are not perforated at all. This is true of the flexor perforatus digiti II in *Chen, Cathartes, Buteo, Falco,* and *Uria;* the flexor perforatus digiti IV and the flexor perforans et perforatus digiti II in *Colaptes* and *Dryobates.*

There is present in many birds a strong vinculum connecting the tendon of the flexor perforatus digiti III with that of the flexor perforans et perforatus digiti III, near the lower end of the tarso-metatarsus. This vinculum is present in *Gavia, Sula, Chen,* domestic duck, *Cathartes, Pedioecetes, Colinus,* domestic fowl, *Grus, Fulica, Totanus, Larus, Zenaidura* and the domestic pigeon. It is absent in *Colymbus, Fregata, Ardea, Buteo, Falco, Uria, Coccyzus, Chordeiles, Chaetura, Bubo, Otus, Colaptes, Dryobates, Tyrannus* and *Corvus.* This structure has heretofore received very little consideration: Gadow (1891, p. 189) mentions it only for *Pterocles.*

In many birds the tendon of the flexor hallucis longus perforates the sheath-like tendon of the flexor hallucis brevis. The latter muscle thus functions as a "flexor perforatus" of the hallux.

Although Garrod (1874a) considered the presence or absence of the ambiens muscle to be of very great taxonomic significance, there is apparently no evidence to support such a view. Several other myological characters in the pelvic limb appear to be fully as important.

The musculature of the pelvic limb in the various species of birds examined shows distinctive peculiarities for each major taxonomic group. In the past students of avian myology have laid too much stress on the presence or absence of certain muscles, with little or no regard to the condition of the muscles that are present.

The exact diagnostic peculiarities of the muscular system in the various orders, families and genera of birds are *yet to be determined.* Avian taxonomists can not hope to reach a final interpretation of the relationships of the different groups while such a state of affairs continues to exist. To the average present-day taxonomist a systematic group of birds is definable almost solely in terms of *feathers and bones.* So much faith has been developed in these easily studied, superficial characters that workers are prone to view with suspicion the great multiplicity of details furnished by myology and the study of the various other "soft parts." The integument and endoskeleton are important within certain limits but constitute, after all, only a small part of the entire morphology of a bird.

REFERENCES

ALIX, E. 1867—Comparaison des os et des muscles des oiseaux avec ceux des mammifères. Bul. de la Soc. philomat.

———1874a—Essai sur l'appareil locomoteur des oiseaux. Paris. Planches I-III.

———1874b—Mémoire sur l' ostéologie et la myologie du Nothura major. J. de Zool. **3**:167-214, 252-282, pls. VIII-XI.

BURT, WILLIAM H. 1930—Adaptive modifications in the woodpeckers. Univ. of Calif. Pub. in Zool. **32**:455-524, 29 figs. in text.

COUES, ELLIOT. 1867—On the osteology and myology of Colymbus torquatus. Mem. Boston Soc. Nat. Hist. **1**:131-172, pl. V.

EYCLESHYMER, ALBERT, C. 1917—Anatomical names. William Wood and Co., New York. 744 pp.

FORBES, W. A. 1881—On the contributions to the anatomy and classification of birds made by the late Prof. Garrod. Ibis. 4 ser., **5**:1-32, figs. 1-9.

———1882—Report on the anatomy of the petrels (Tubinares), collected during the voyage of H. M. S. Challenger. Zoology **4**:1-64, pls. I-VII.

GADOW, HANS. 1880—Zur vergleichenden Anatomie der Muskulatur des Beckens und der hinteren Gliedmasse der Ratiten. pp. 1-56, pls. 5. Jena.

———1882a—On some points in the anatomy of Pterocles, with some remarks on its systematic position. Proc. Zool. Soc. London: 312-332, figs. 1, 2.

———1882b—Observations in comparative myology. J. Anat. and Physiol. **16**:493-514.

———UND EMIL SELENKA. 1891—Vögel, vol. I, Anatomischer Theil. *In* Bronn's Klassen und Ordnungen des Thier-Reichs, Sechster Band, Vierte Abtheilung, 1008 pp., 59 pls. Leipzig.

GARROD, ALFRED H. 1873—On certain muscles in the thigh of birds, and their value in classification. Part I. Proc. Zool. Soc. London: 626-644, figs. 1-6.

———1874a—On certain muscles in the thigh of birds and their value in classification. Part II. Ibid. :111-123.

———1874b—On some points in the anatomy of the Columbae. Ibid. :249-259.

———1874c—On some points in the anatomy of the parrots which bear on the classification of the suborder. Ibid. :586-598, pls. LXX-LXXI.

———1875—On the disposition of the deep plantar tendons in different birds. Ibid. :339-348, figs. 1-9.

———1877—Notes on an anatomical peculiarity in certain storks. Ibid. :711-712.

———1879—Notes on points in the anatomy of the hoatzin (Opisthocomus cristatus). Ibid. :109-114.

———1881—The collected scientific papers of the late Alfred Henry Garrod. W. A. Forbes, ed. London.

GUYER, M. F. 1930—Animal micrology. Univ. of Chicago Press.

HASWELL, W. A. 1880—The myological characters of the Columbidae. Proc. Linn. Soc. New South Wales **4**:306.

———1883—The myological characters of the Columbidae. Ibid. **7**:218-221, 404.

HAUGHTON, SAMUEL. 1865—On the muscular mechanism of the leg of the ostrich. Ann. & Mag. Nat. Hist., 3rd ser., **15**:262-272, pls. VI-VII.

———1868a—Muscular anatomy of the emu. Proc. Roy. Irish Acad. **9**:487-497.

———1868b—Muscular anatomy of the rhea. Ibid. **9**:497-504.

———1868c—On the comparative myology of certain birds. Ibid. **9**:524-526.

KLEMM, F. 1864—Zur Muskulatur der Raben. Zeitschr. ges. Naturw. **23**. Berlin.

DE MAN, J. G. 1873—Vergelijkende myologische en neurologische Studien over Amphibien en Vögels. Academisch Proefschrift. 4 taf., pls. III-IV. Leiden.

MARSHALL, MARGARET E. 1905—A study of the anatomy of Phalaenoptilus Ridgway. Proc. Am. Philos. Soc. **44**:213-240, pls. IV-VI.

MECKEL, J. F. 1825—System der vergleichenden Anatomie. **3**. Halle.

———1830—Beiträge zur Anatomie des indischen Kasuars. Meckel's Archiv für Anat. u. Phys. Leipzig.

NITZSCH-GIEBEL. 1857—Beiträge zur Anatomie der Möven. Zeitschr. ges. Naturw. **10**:20-32.

———1862—Zur Anatomie der Papageien. Zeitschr. ges. Naturw. **19**:133-150, pls. III-VII.

OWEN, RICHARD. 1835—Article on Aves in Todd's Cyclopaedia of anatomy and physiology **1**:290. London.

———1849—On the anatomy of the southern Apteryx. Trans. Zool. Soc. London **3**:277.

RIDGWAY, ROBERT. 1919—Birds of North and Middle America. Part 8. U. S. Nat. Mus. Bull. **50**.

SABATIER, A. 1880—Comparaison des ceintures et des membres antérieurs et postérieurs dans la série des vertébrés. Montpellier and Paris. 4 Extrait des mémoires de l'Academie des Sciences et Lettres, Section des Sciences, **9**.

SELENKA, EMIL. 1869—Vögel. *In* Bronn's Klassen und Ordnungen des Thier-Reichs.

SHUFELDT, R. W. 1886—Contributions to the anatomy of Geococcyx californianus. Proc. Zool. Soc. London :466-490, pls. XLII-XLV, 2 wcc. in text.

———1890—The myology of the raven (Corvus corax sinuatus). 343 pp., 76 figs. in text. Macmillan & Co., London.

SUNDEVALL, C. J. 1851—Om Muskelbyggnaden i foglarnas extremiteter. Förhandl. vid. Skandin. Naturforskarnes. 6 Moete, 9.

TIEDEMANN, FR. 1810—Zoologie, **2**: Anatomie und Naturgeschichte der Vögel. Heidelberg.

VICQ D'AZYR. 1772-1778—Mémoires pour servir à l'anatomie des oiseaux. Mém. de l'Acad. Royale des Sciences, Paris **1772**:617-633; **1773**:566-586; **1774**: 489-521; **1778**:381-392.

WATSON, MORRISON. 1869—On the mechanism of perching in birds. J. Anat. and Physiol. **3**:379-384.

——1883—Report on the anatomy of the Spheniscidae. *In* Zoölogy of the voyage of the Challenger, **18**.

WELDON, W. F. R. 1883—On some points in the anatomy of Phoenicopterus and its allies. Proc. Zool. Soc. London :638-652, pls. 59, 60.

LIST OF ABBREVIATIONS

Abd. dig. II	M. abductor digiti II
Abd. d. IV	M. abductor digiti IV
Abd. mus.	Abdominal muscle
Acc.	Accessorius semitendinosi
Add. d. II	M. adductor digiti II
Add. d. IV	M. adductor digiti IV
Add. long.	M. adductor longus et brevis
Ambiens	M. ambiens
Bic. fem.	M. biceps femoris
Bic. loop	Biceps loop
Cart.	Cartilage
Dig.	Digit
Ext. brev. d. III	M. extensor brevis digiti III
Ext. brev. d. IV	M. extensor brevis digiti IV
Ext. dig. brev.	M. extensor digitorum brevis
Ext. dig. l.	M. extensor digitorum longus
Ext. hal. l.	M. extensor hallucis longus
Ext. pro. d. III	M. extensor proprius digiti III
Fem.	Femur
Fem. tib.	M. femori-tibialis
Fem. tib. ext.	M. femori-tibialis externus
Fem. tib. int.	M. femori-tibialis internus
Fem. tib. med.	M. femori-tibialis medius
Fib.	Fibula
F. dig. l.	M. flexor digitorum longus
F. hal. brev.	M. flexor hallucis brevis
F. hal. l.	M. flexor hallucis longus
F. p. et p. d. II	M. flexor perforans et perforatus digiti II
F. p. et p. d. III	M. flexor perforans et perforatus digiti III
Flex. per. d. II	M. flexor perforatus digiti II
Flex. per. d. III	M. flexor perforatus digiti III
Flex. per. d. IV	M. flexor perforatus digiti IV
Gas.	M. gastrocnemius
Glut. max.	M. glutaeus maximus
Glut. med. et min.	M. glutaeus medius et minimus
Iliacus	M. iliacus
Il. tib.	M. ilio-tibialis
Il. tib. ant.	M. ilio-tibialis anterior
Il. troc. ant.	M. ilio-trochantericus anterior
Il. troc. med.	M. ilio-trochantericus medius
Il. troc. post.	M. ilio-trochantericus posterior
Isch.	Os ischii
Isch. fem.	M. ischio-femoralis
Lumb.	M. lumbricalis
Met. I	Os metatarsale I
Met. II	Os metatarsale II
Met. III	Os metatarsale III
Met. IV	Os metatarsale IV

Mm. flex. per. dig.	Mm. flexores perforati digiti II, III, IV
Mm. flex. per. et per.	Mm. flexores perforantes et perforati digiti II, III
Mm. il. troc.	Mm. ilio-trochanterici
Obt. ext.	M. obturator externus
Obt. int.	M. obturator internus
P. ant.	Pars anterior
P. caud. fem.	Pars caudi-femoralis
P. ext.	Pars externa
P. il. fem.	Pars ilio-femoralis
P. int.	Pars interna
P. med.	Pars media
P. post.	Pars posterior
Pat. ten.	Patellar tendon
Per. brev.	M. peronaeus brevis
Per. long.	M. peronaeus longus
Phal.	Phalanx
Pirif.	M. piriformis
Plan.	M. plantaris
Pop.	M. popliteus
Pub.	Os. pubis
Sar.	M. sartorius
Semim.	M. semimembranosus
Semit.	M. semitendinosus
Tar.-met.	Tarso-metatarsus
T. fas. lat.	M. tensor fasciae latae
Tib.	Tibia
Tib. ant.	M. tibialis anterior
Tib. cart.	Tibial cartilage

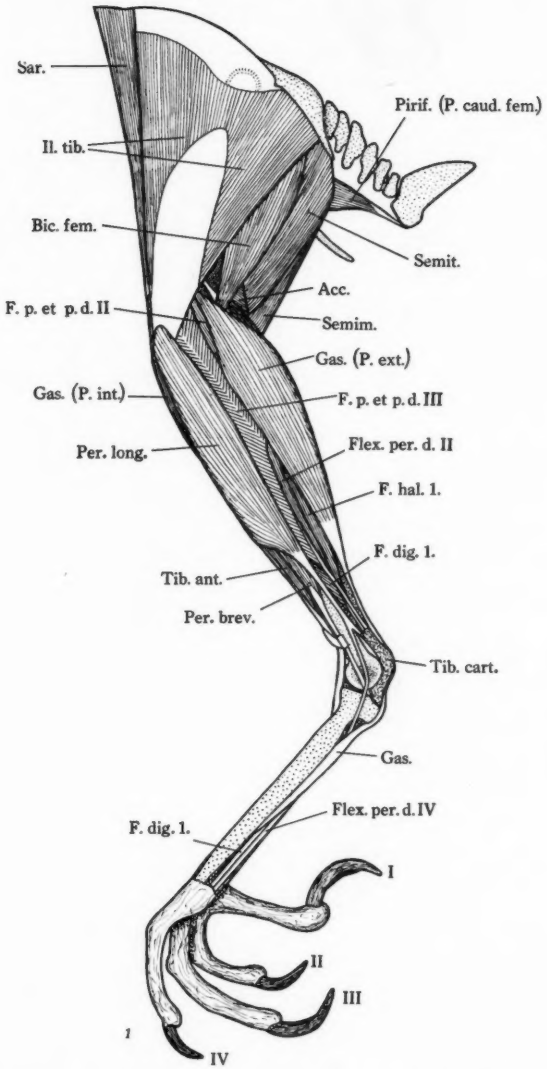


Fig. 1. Crow. Superficial muscles of the left leg (lateral view). x .75.

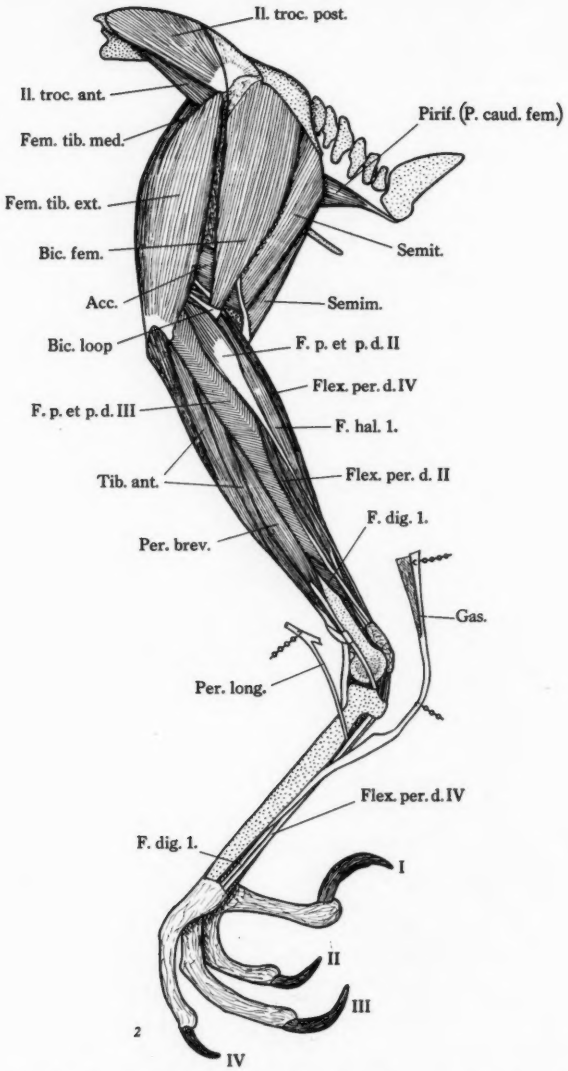


Fig. 2. Crow. External view of left leg showing a second layer of muscles. The following superficial muscles have been wholly or partly removed: Sar., Il. tib., Gas., Per. long. x .75.

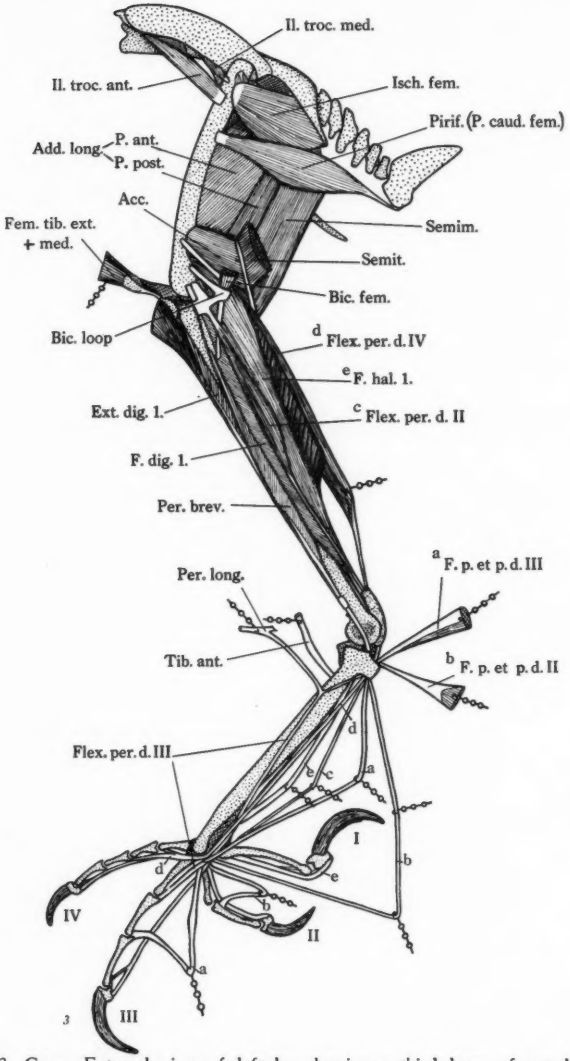


Fig. 3. Crow. External view of left leg showing a third layer of muscles. In addition to those listed for Plate 2 the following have also been wholly or partly removed: Bic. fem., Fem. tib. ext. + med., Semit., Il. troc. post., Tib. ant., F. p. et p. d. II. F. p. et p. d. III. NOTE: In this figure the tendons of insertion of the Ext. dig. 1. have been omitted to avoid confusion; they are shown in detail on Plate 4. x .75.

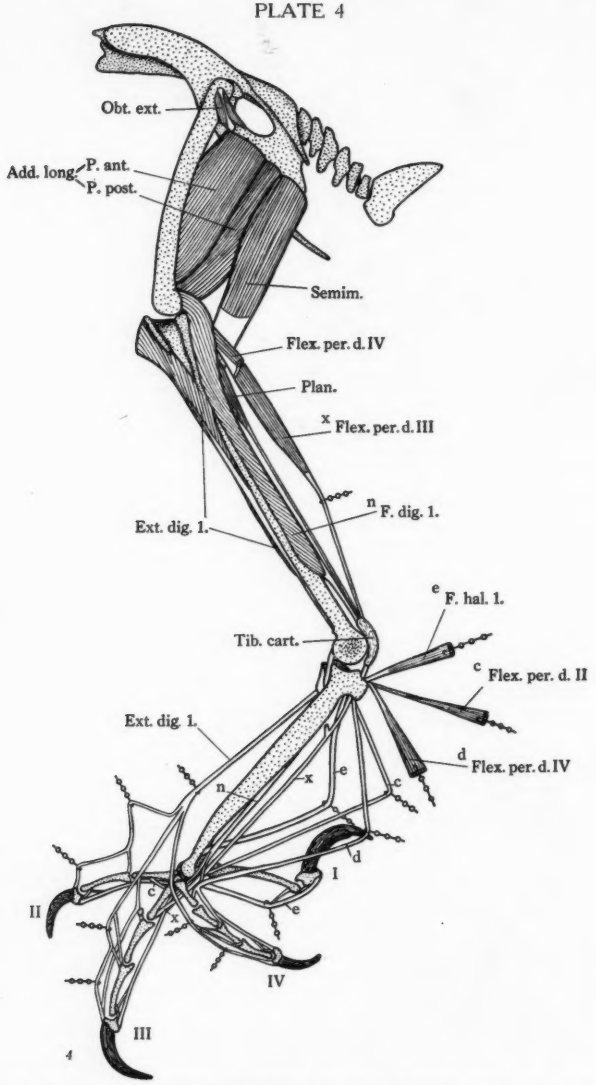


Fig. 4. Crow. External view of left leg showing a fourth layer of muscles. In addition to those listed for Plate 3 the following have also been wholly or partly removed: Isch. fem., Il. troc. ant., Pirif., Semit., Acc., Per. brev., Flex. per. d. II, Flex. per. d. IV, F. hal. 1 x .75.

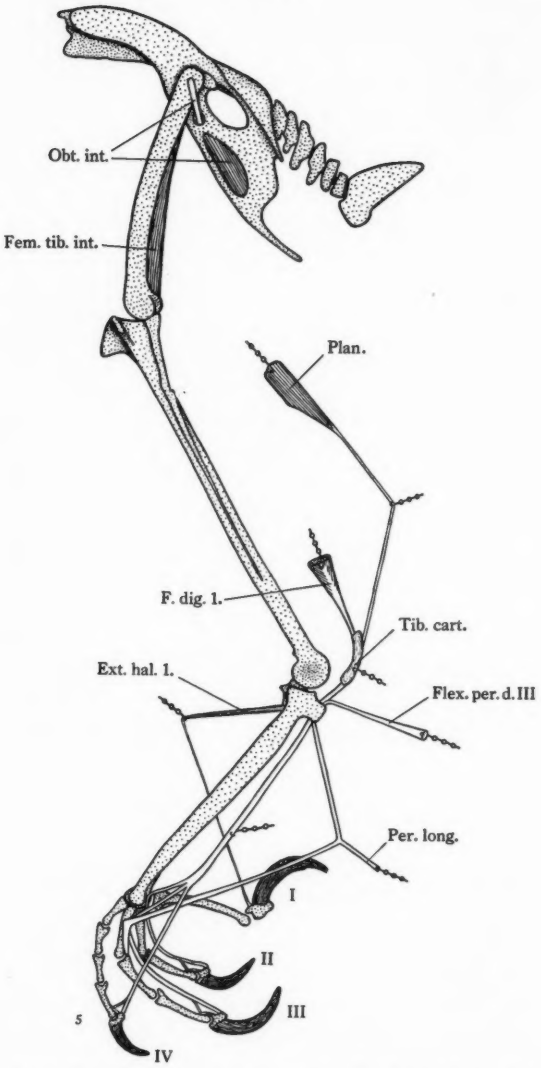


Fig. 5. Crow. External view of left leg showing the deepest layer of muscles. In addition to the ones listed for Plate 4 the following have also been wholly or partly removed: F. dig. 1., Plan., Flex. per. d. III, Obt. ext., Add. long. x .75.

PLATE 6

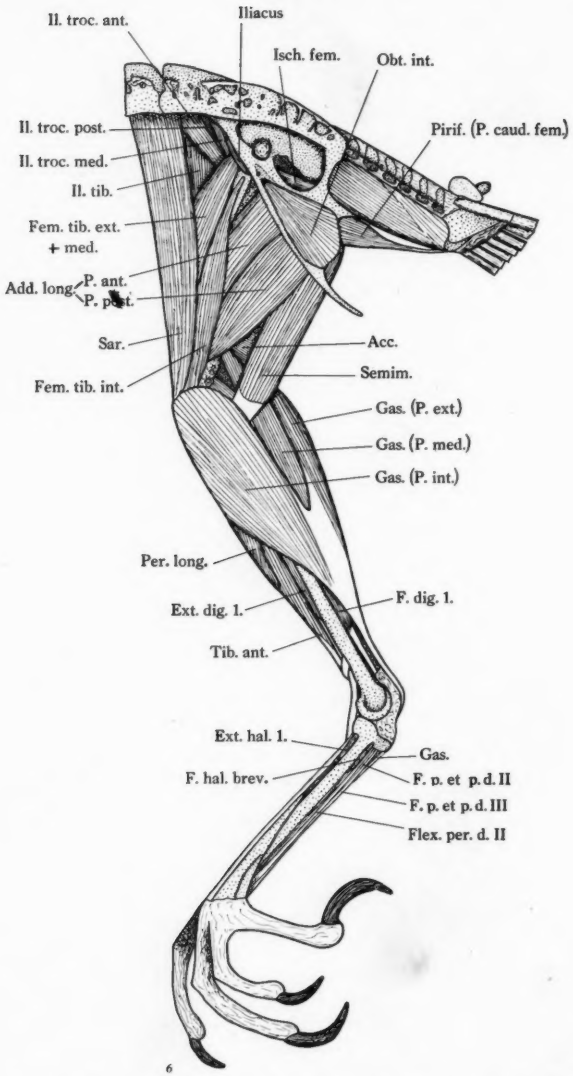


Fig. 6. Crow. Medial view of right leg showing the superficial muscles. The viscera, abdominal muscles and left side of the pelvis and vertebral column have been removed. x .7.

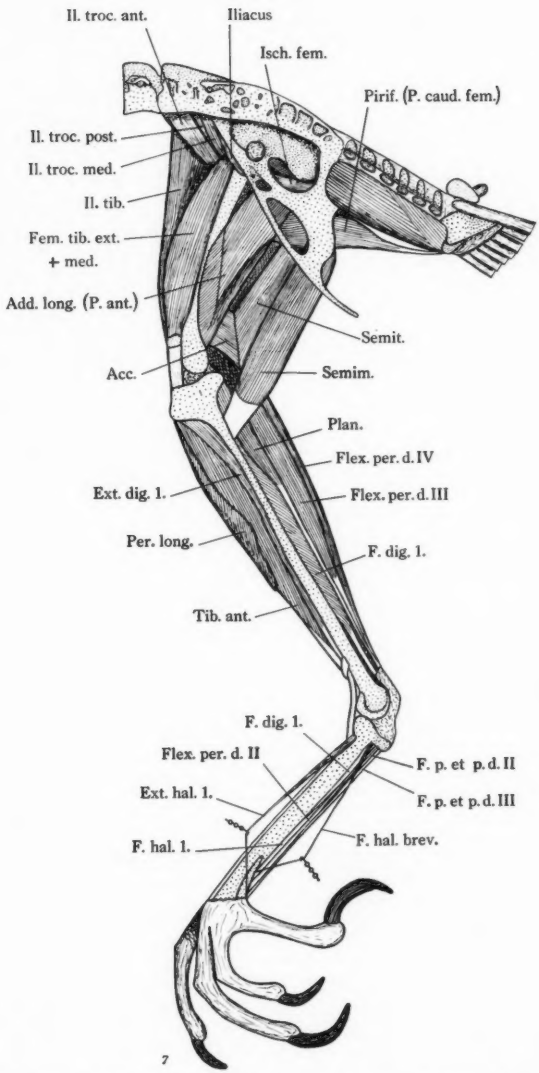


Fig. 7. Crow. Medial view of right leg showing a second layer of muscles. The following superficial muscles have been removed: Sar., Fem. tib. int., Add. long. (P. post.), Obt. int., Gas. x .7.

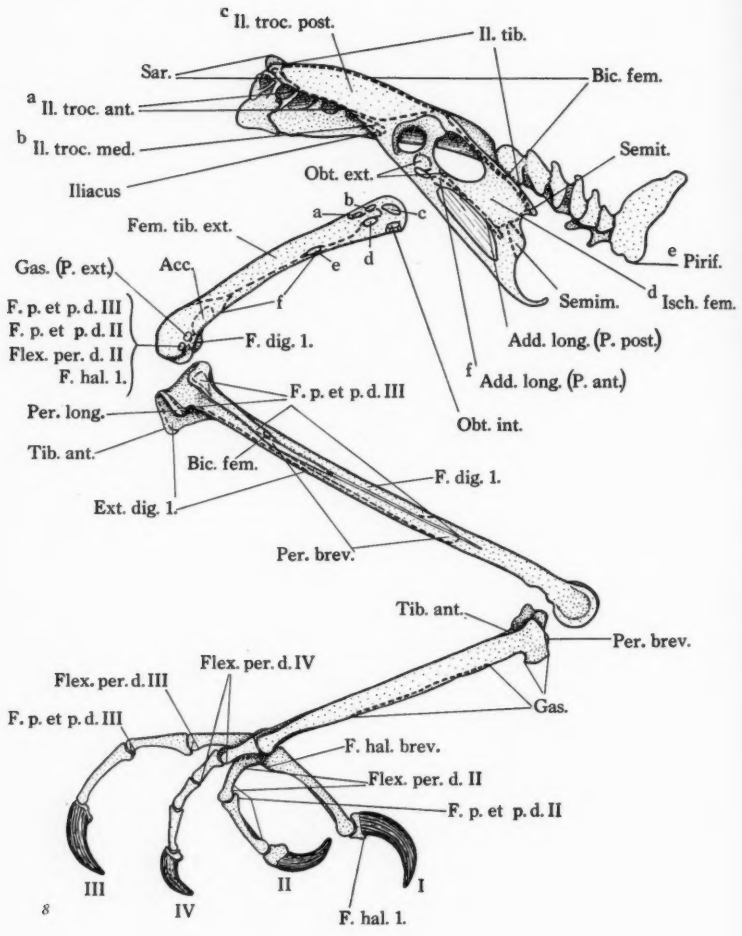


Fig. 8. Crow. External view of bones of the left leg and pelvis showing areas for muscle attachments. The principal bones are disarticulated. NOTE: Certain attachments are marked with letters which conform with similar letters placed in front of the corresponding muscle label. This was done to reduce crowding. x .8.

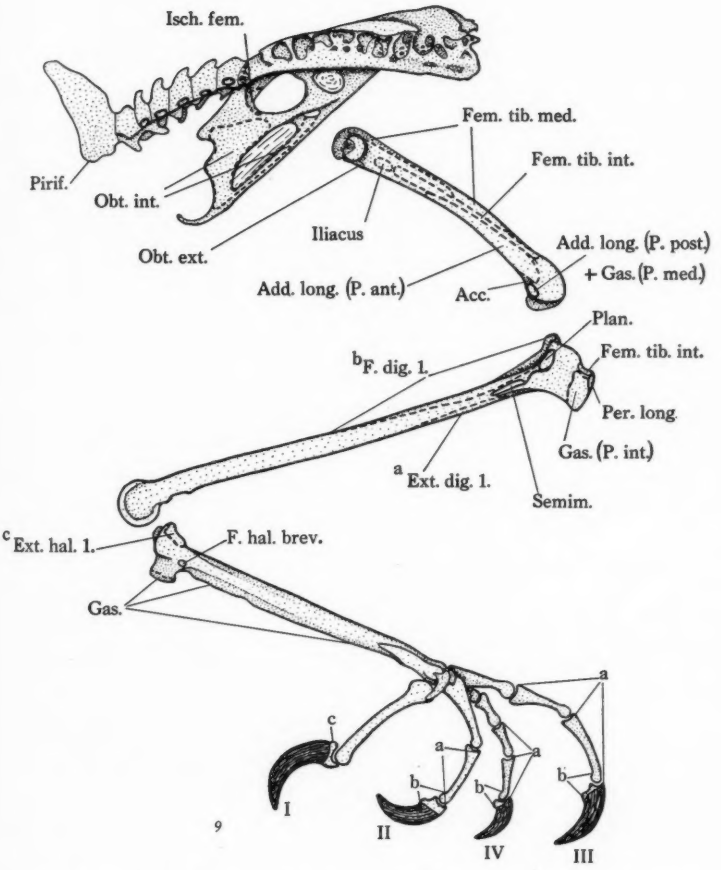


Fig. 9. Crow. Medial views of the bones of the left leg showing areas for muscle attachments. The principal bones are disarticulated. NOTE: Certain attachments are marked with letters which conform with similar letters placed in front of the corresponding muscle label. This was done to reduce crowding. x .8.

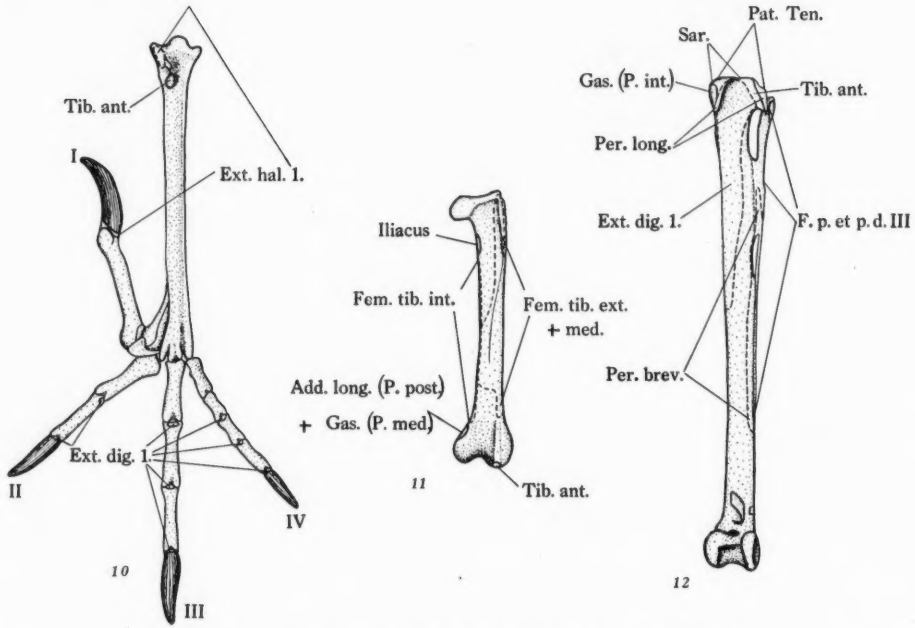
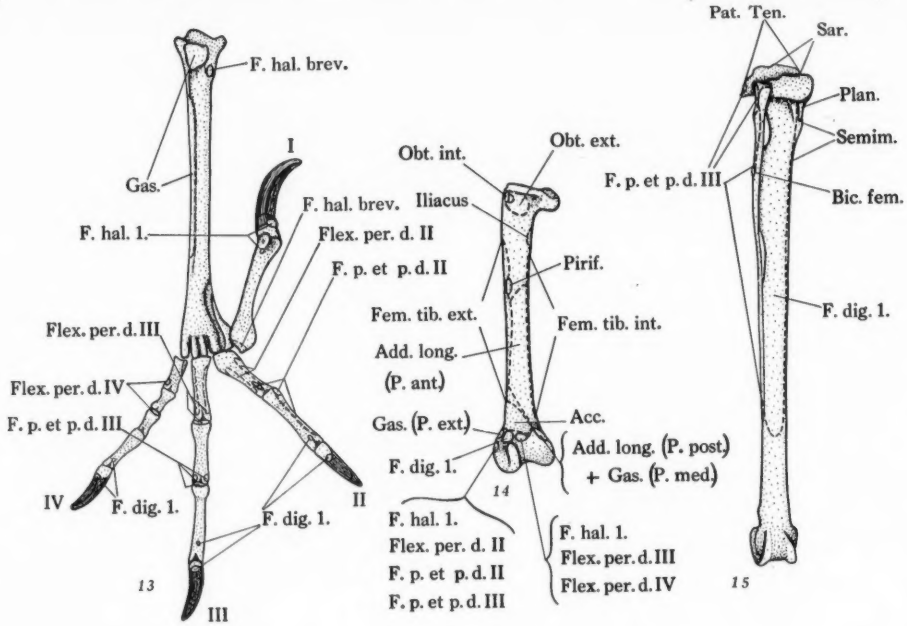


Fig. 10. Tarso-metatarsus and digits. Fig. 11. Femur. Fig. 12. Tibio-tarsus.
Crow. Anterior views of the bones of the left leg showing areas for muscle attachments. x .8.

Crow. Anterior views of the bones of the left leg showing areas for muscle attachments. x .8.



Crow. Posterior views of the bones of the left leg showing areas for muscle attachments. x .8. Fig. 13. Tarso-metatarsus and digits. Only the main points of attachment are shown for the gastrocnemius. Fig. 14. Femur. Fig. 15. Tibio-tarsus.

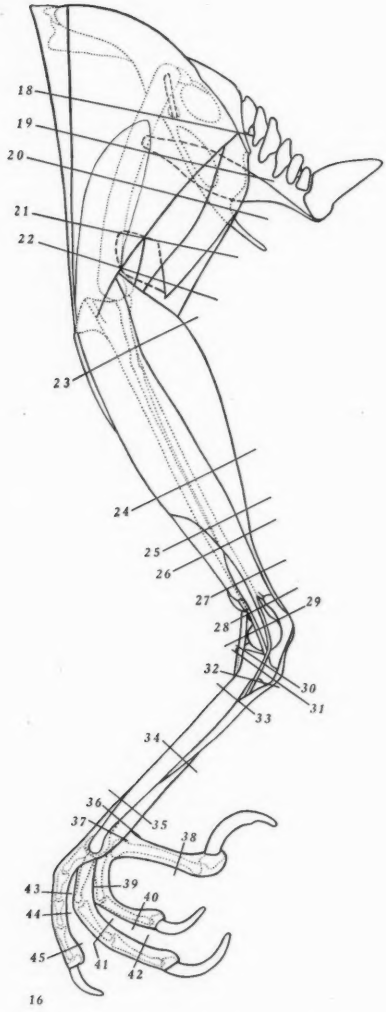


Fig. 16. Crow. Diagram of the left pelvic appendage (lateral view) to show the horizons from which the various cross sections were cut. The numbers refer to the figure numbers of the respective cross sections. x .7.

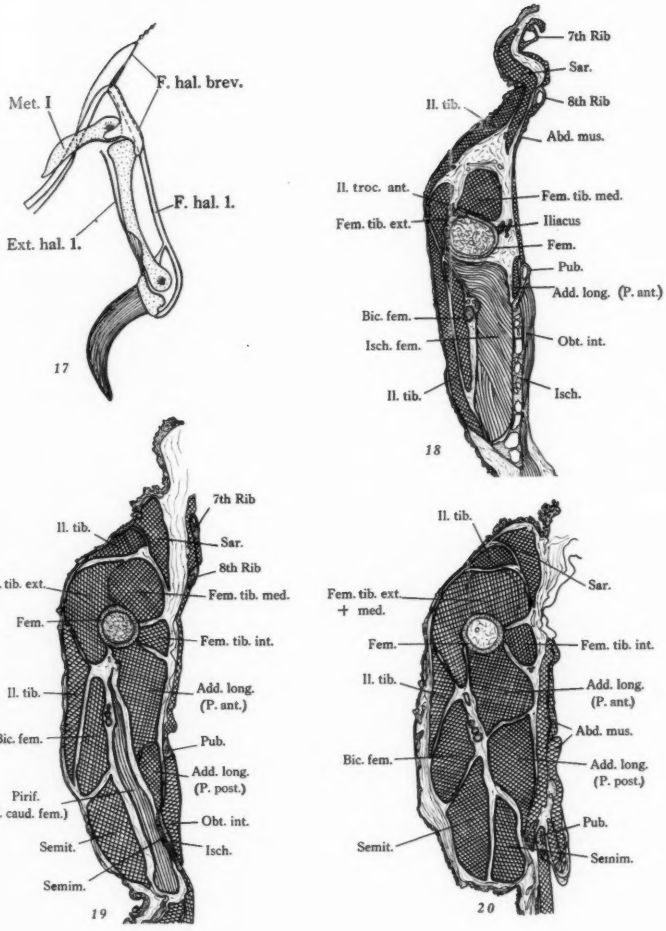
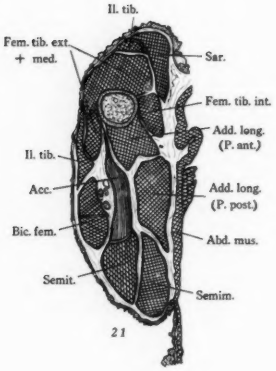
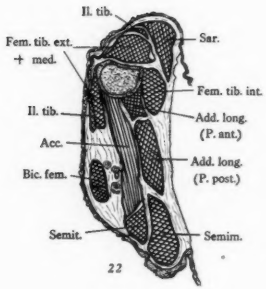
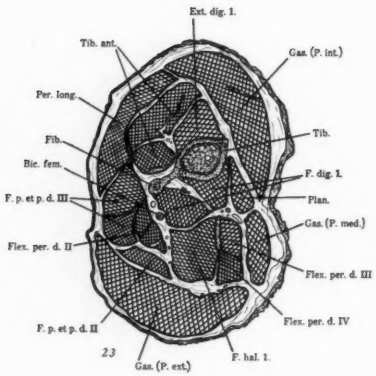
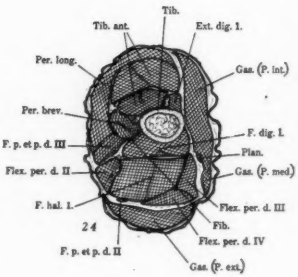


Fig. 17. Crow. Medial view of left hallux showing the insertion of the F. hal. brev. x 1. Fig. 18. Crow. Cross section of the thigh. About one-fourth the way down the femur. x 1.5. In all of the cross section drawings the top of the page corresponds to the anterior side of the section, the bottom to the posterior side. Right and left sides of the page coincide with the same sides of the section. Fig. 19. Cross-section of thigh. About one-third the way down the femur. x 1.5. Fig. 20. Cross section of thigh. About midway the femur. x 1.5.



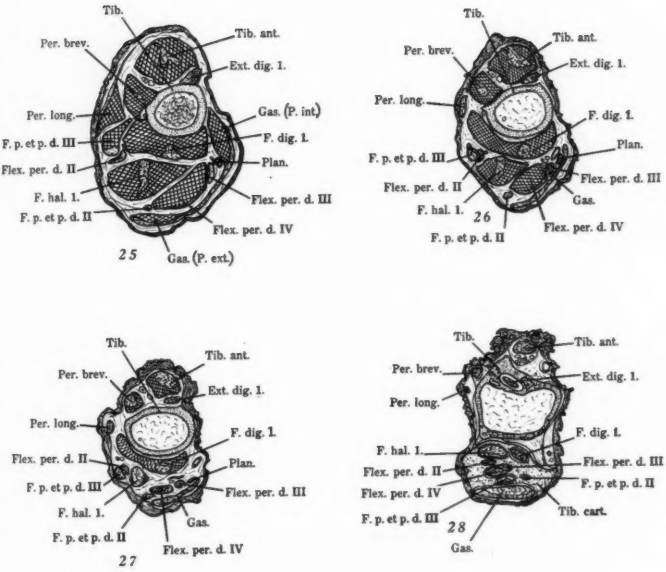






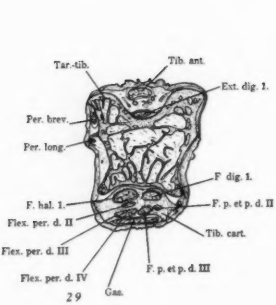
Crow sections.

Fig. 21. About three-fourths the way down the femur. x 1.3.
Fig. 22. Just above the femoral condyles. x 1.3.
Fig. 23. About one-sixth the way down the tibio-tarsus. x 1.8.
Fig. 24. About half-way down the tibio-tarsus. x 1.8.

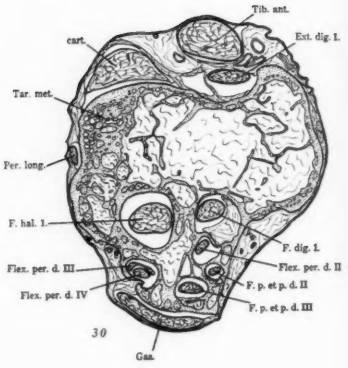


Crow. Shank sections. x 2.

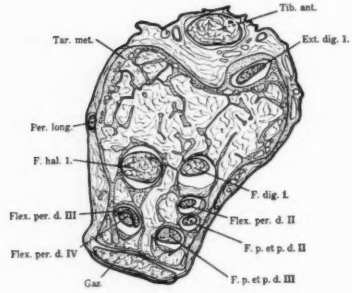
Fig. 25. About two-thirds the way down the tibio-tarsus.
Fig. 26. About six-eighths the way down the tibio-tarsus.
Fig. 27. About five-sixths the way down the tibio-tarsus.
Fig. 28. Just above the distal malleoli.



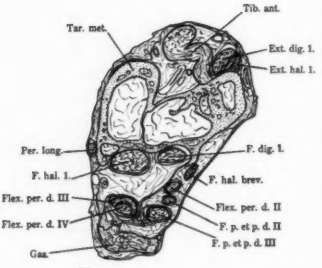
29



30



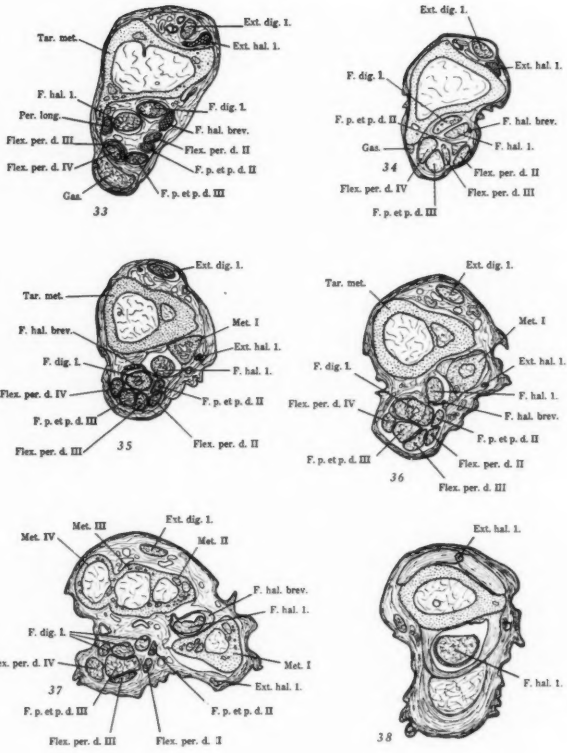
31



32

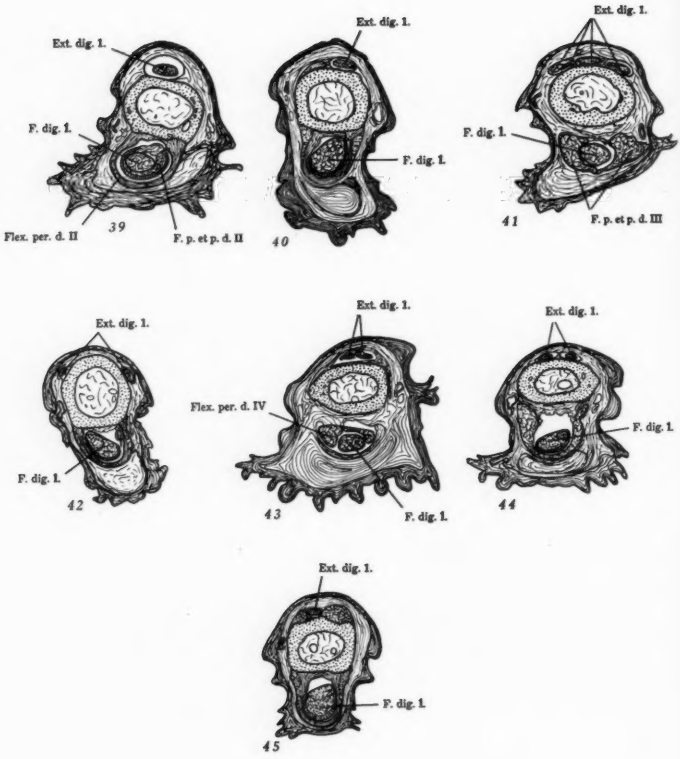
Crow. Sections of the distal end of the tibio-tarsus and the proximal end of the tarso-metatarsus.

Fig. 29. Through the distal malleoli of the tibio-tarsus. x 2.
Fig. 30. Extreme proximal end of tarso-metatarsus. x 4.
Fig. 31. About midway the perforated process. x 4.
Fig. 32. Through the point of insertion of the *M. tib. ant.* x 4.



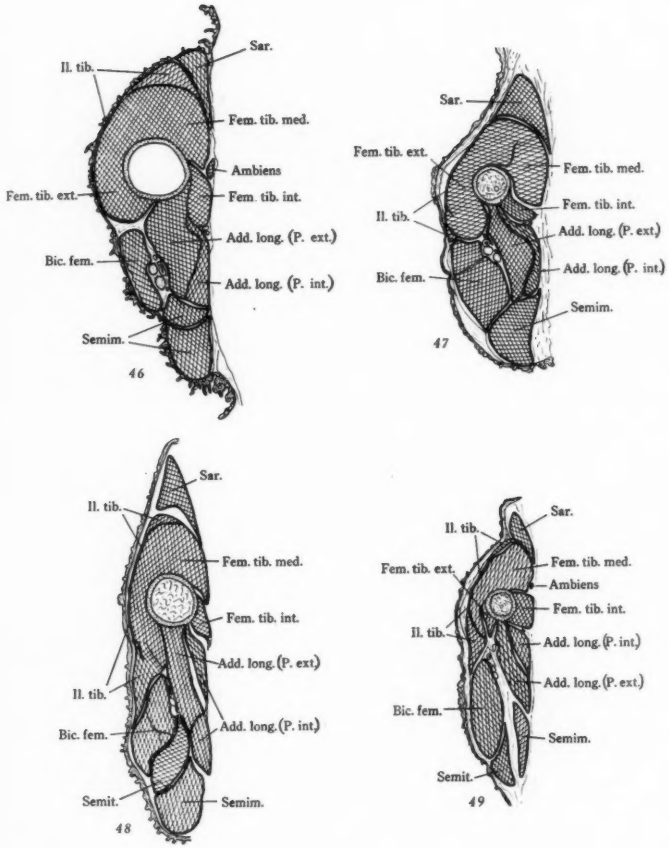
Crow. Sections of the tarso-metatarsus and hallux.

Fig. 33. About one-fifth the way down the tarso-metatarsus. x 3.
Fig. 34. About midway the tarso-metatarsus. x 3.
Fig. 35. About three-fourths the way down the tarso-metatarsus. x 3.
Fig. 36. About seven-eighths the way down the tarso-metatarsus. x 3.
Fig. 37. Just above the distal malleoli of the tarso-metatarsus. x 3.
Fig. 38. Near the distal end of the proximal phalanx of the hallux. This digit is shown as rotated forward into the primitive position. x 5.



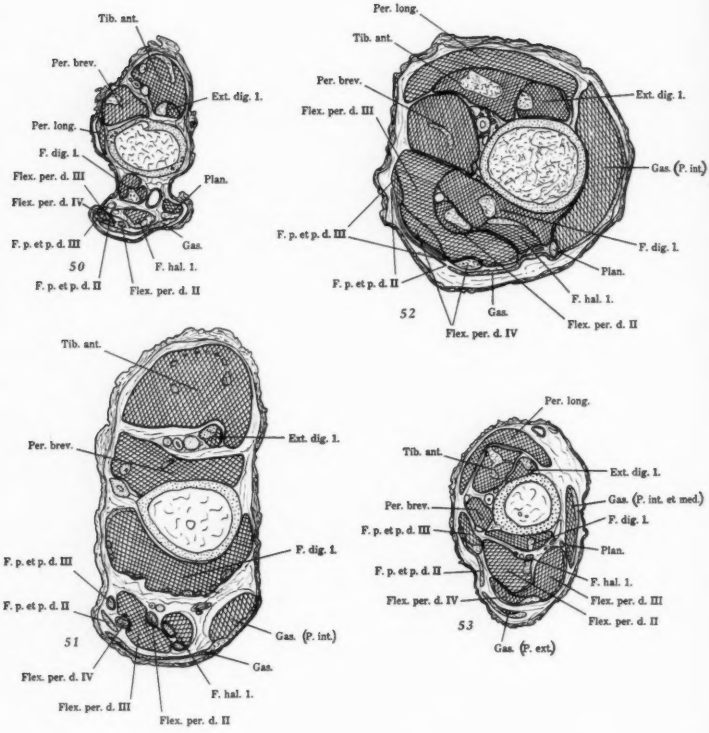
Crow. Sections of the various phalanges of the fore-toes. x 5.

Fig. 39. Proximal phalanx of index digit.
Fig. 40. Second phalanx of index digit.
Fig. 41. Second phalanx of third digit.
Fig. 42. Third phalanx of third digit.
Fig. 43. Second phalanx of fourth digit.
Fig. 44. Third phalanx of fourth digit.
Fig. 45. Fourth phalanx of fourth digit.



Sections of the thigh taken from about the middle of the femur.

Fig. 46. Sparrow hawk *(Falco sparverius)*. x 4.
Fig. 47. Screech owl *(Otus asio)*. x 2.
Fig. 48. Green heron *(Butorides virescens)*. x 2.5.
Fig. 49. Lesser yellowlegs *(Totanus flavipes)*. x 2.5.



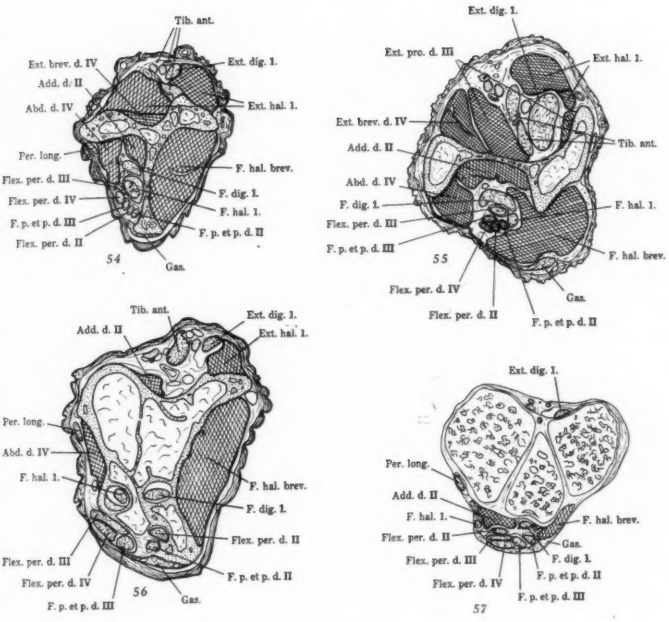
Sections of the shank taken near the distal end of the carneous portions of the muscles.

Fig. 50. Sparrow hawk *(Falco sparverius)*. About four-fifths the way down the tibio-tarsus. x 5.

Fig. 51. Screech owl *(Otus asio)*. About two-thirds the way down the tibio-tarsus. x 6.

Fig. 52. Green heron *(Butorides virescens)*. About midway the tibio-tarsus. x 5.5.

Fig. 53. Lesser yellowlegs *(Totanus flavipes)*. About one-fourth the way down the tibio-tarsus. x 6.



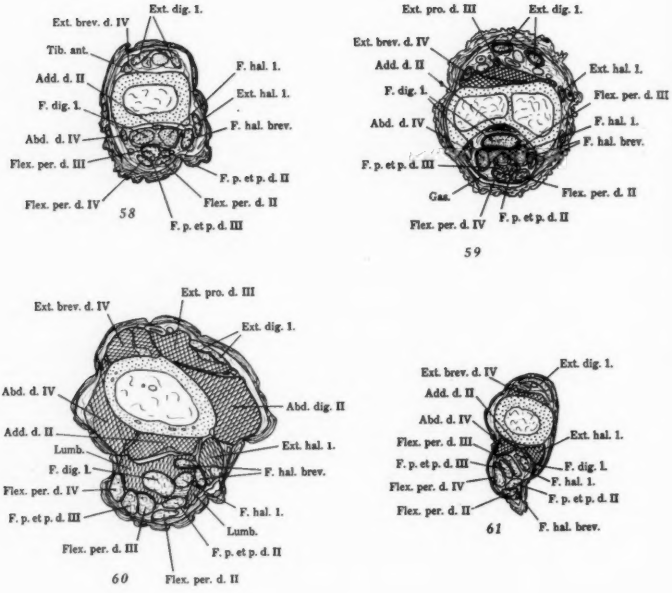
Sections of the proximal portion of the tarso-metatarsus. x 6.

Fig. 54. Sparrow hawk *(Falco sparverius)*. About one-sixth the way down the tarso-metatarsus.

Fig. 55. Screech owl *(Otus asio)*. About one-fifth the way down the tarso-metatarsus.

Fig. 56. Green heron *(Butorides virescens)*. About one-tenth the way down the tarso-metartarsus.

Fig. 57. Lesser yellowlegs *(Totanus flavipes)*. About one-tenth the way down the tarso-metatarsus.



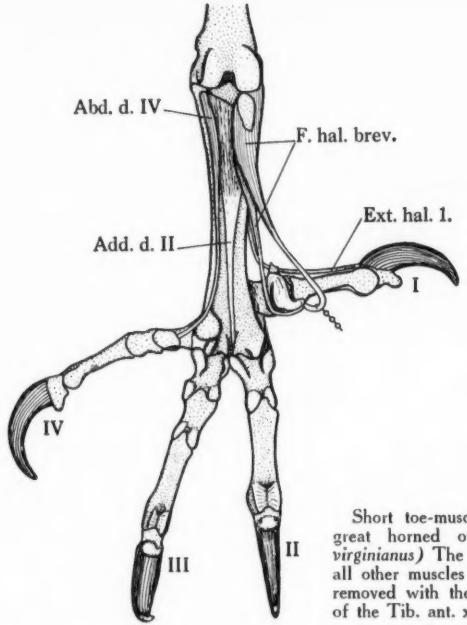
Sections of the distal portion of the tarso-metatarsus.

Fig. 58. Sparrow hawk *(Falco sparverius)*. About two-thirds the way down the tarso-metatarsus. x 6.

Fig. 59. Screech owl *(Otus asio)*. About midway the tarso-metatarsus. x 5.

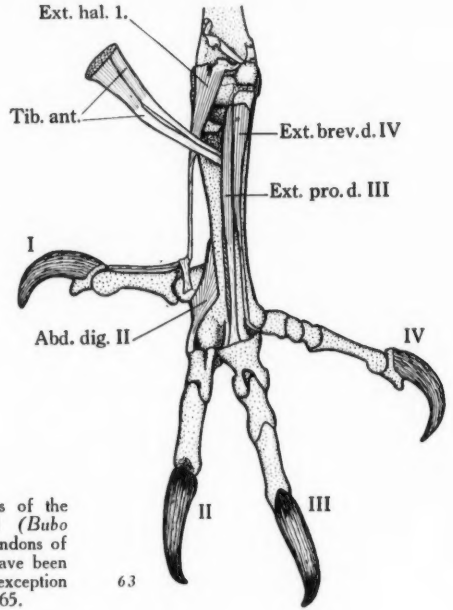
Fig. 60. Green heron *(Butorides virescens)*. About four-fifths the way down the tarso-metatarsus. x 6.

Fig. 61. Lesser yellowlegs *(Totanus flavipes)*. About two-thirds the way down the tarso-metatarsus. x 6.



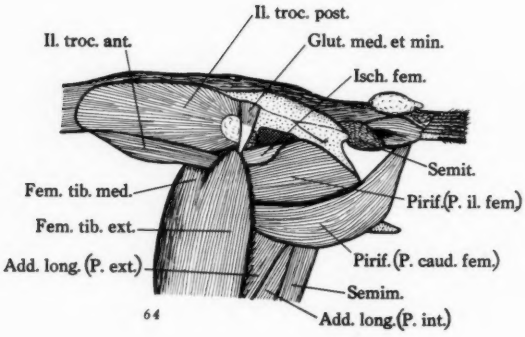
62

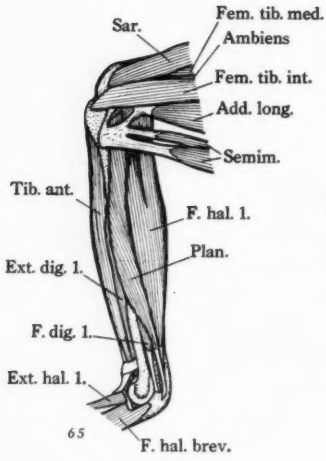
Short toe-muscles of the great horned owl *(Bubo virginianus)* The tendons of all other muscles have been removed with the exception of the Tib. ant. x .65.



63

Fig. 62. Posterior view of the tarso metatarsus and digits.
Fig. 63. Anterior view of the tarso-metatarsus and digits. Note the double insertion of the Tib. ant.





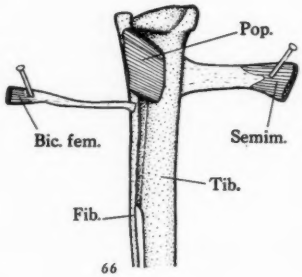
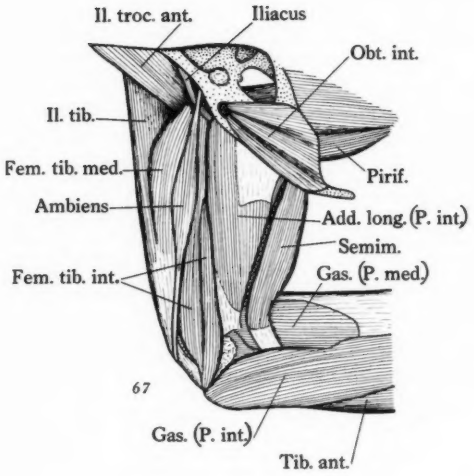
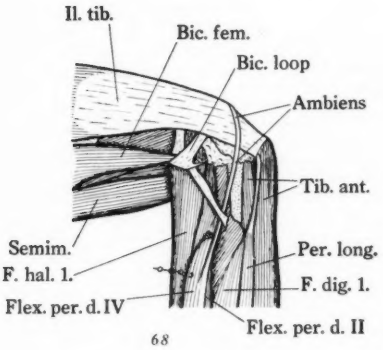


Fig. 64. Lateral view of the left side of the pelvic region of the bob-white *(Colinus virginianus)*. Drawn to show especially the two parts of the *M. piriformis* and the *M. glutaeus medius et minimus*. The following have been removed: Sar., Il. tib., and Bic. fem. All of the Semit. has been removed except the stub of the origin. x 1.

Fig. 65. Medial view of the right shank of the sparrow hawk *(Falco sparverius)*. Drawn to show especially the well developed *M. plantaris* and the double *M. semimembranosus*. *M. gas.* removed. x 1.

Fig. 66. Posterior view of the proximal end of the tibia and fibula of the great horned owl *(Bubo virginianus)*. To show the deeply situated *M. popliteus*. x .75.

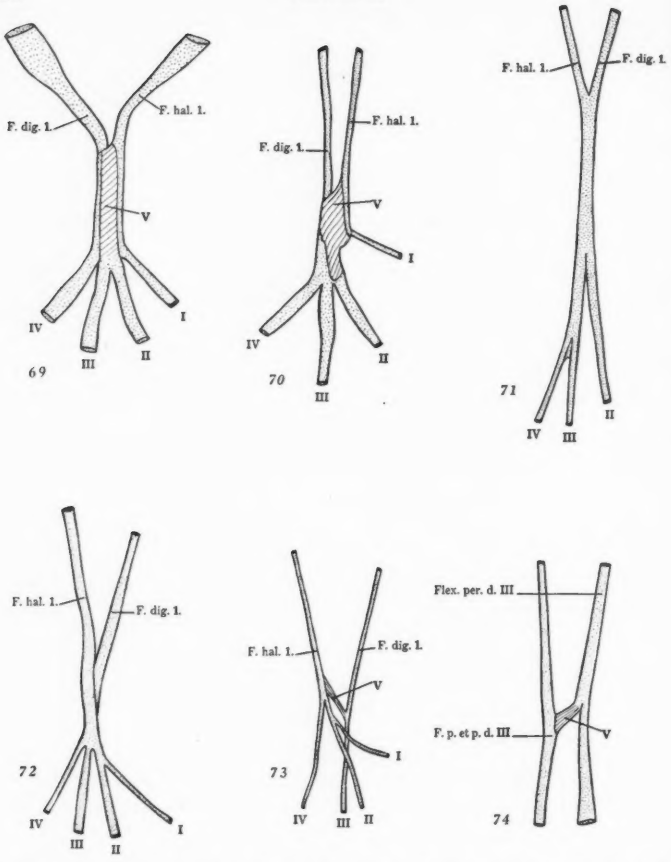




Drawn to show especially the *M. ambiens* in the Swainson's hawk *(Buteo swainsoni)*. x .75.

Fig. 67. Medial view of the right thigh. *M. sartorius* removed.

Fig. 68. Lateral view of the right knee region. The following muscles have been removed: Gas., F. p. et p. d. II, and F. p. et p. d. III. The tendinous lateral head of origin of the Flex. per d. IV has also been removed so as to expose more fully the tendon of the ambiens. NOTE: The patellar tendon has been slit open directly over the tendon of the ambiens and the latter lifted out and placed upon the incision.



Showing the connections between certain flexor tendons in the foot of various birds. Whenever a *vinculum* is present it is indicated by the letter "V." The Roman numerals refer to the tendons supplying the corresponding toes. In most cases the tendons are displaced so as to better expose the connections.

Fig. 69. Great horned owl *(Bubo virginianus)*. Showing the extensive vinculum connecting the two deep flexor tendons. x .8 Fig. 70. Sharp-tailed grouse *(Pedioecetes phasianellus)*. Showing the vinculum connecting the two deep flexor tendons. x 1.5. Fig. 71. Common loon *(Gavia immer)*. Showing the fusion of the two deep flexor tendons. There is no branch to the hallux. x 1. Fig. 72. Man-o'-war- bird *(Fregata magnificens)*. Showing the fusion of the deep flexor tendons. x 1. Fig. 73. Flicker *(Colaptes auratus)*. The F. dig. 1. is undivided and supplies the third toe, the F. hal. 1. trifurcating to supply digits I, II, and IV. Slightly enlarged. Fig. 74. Little brown crane *(Grus canadensis)*. Showing the vinculum connecting the tendons of the two superficial flexors to the third toe. x 1.

Aulopora: a Form-Genus of Tabulate Corals and Bryozoans[1]

Mildred Adams Fenton and Carroll Lane Fenton

I. Introduction; Summary

In studying Auloporoid fossils from the Devonian of Iowa and Michigan, we had difficulty in determining whether certain small forms were "tabulate" corals or large bryozoans belonging to the group of prostrate genera typified by *Stomatopora* and *Hederella*. This difficulty caused the senior author to question [2,3] the coralline affinities of *Aulopora* itself, and to suggest that it was a member of the bryozoan family *Diastoporidae*.

Final publication was delayed, to await the sectioning of authentic specimens of *Aulopora serpens* Goldfuss, the genotype, and solution of taxonomic problems presented by certain species essential to the argument. The former showed that *Aulopora*, if strictly limited, must stand as a coralline genus; the latter, and examination of other material, showed with equal conclusiveness that several species described as *Aulopora* are, or may be, bryozoans. Since it is not yet possible to make a definite division of the genus, this paper merely reviews the evidence at hand, suggests that until it can properly be divided, *Aulopora* be regarded as a form-genus containing both tabulate corals and bryozoans, and indicates some described species which are most clearly linked with the latter phylum. A more definite course must await comprehensive treatment of the form-genus and similar but undoubted bryozoa.

II. Descriptions

Aulopora Goldfuss, 1826

Genotype: *Aulopora serpens* Goldfuss

Goldfuss, Petref. Germ. **1**:82, 1826.

Original Description.—

Stirps calcarea, e tubulis obconicis, vacuis, e latere proliferis, singulis ostiolis terminalibus exsertis.

Der Polypenstock besteht aus kleinen, kalkartigen, verkehrt-kegelförmigen Röhrchen, welche sich durch Aussprossen aus ihren Seitenwänden vervielfältigen, und dadurch theils ein Netz, theils einen ähren-oder büschelförmigen Stamm bilden. Sie haben weder Sternlamellen noch Querwände, und ihre Höhlungen stehen unter sich in Verbindung, sind jedoch da, wo ein Röhrchen aus der Seite des andern hervortritt, sehr verengt. Jedes Röhrchen hat seine eigene, runde oder ovale, vorragende Mündung.

Sie stehen entweder frei, oder überziehen als Schmarotzer andere Korallen.

---

1 Completion of this study was made possible by a grant from the Elizabeth Thompson Science Fund. Four of the plates illustrating it and the following paper were provided by the University of Cincinnati Museum.

2 Ohio Acad. Sci. Proc. **8**(4):172, 1922; Ohio Jour. Sci. **28**:150, 1928.

3 Bull. Geol. Soc. Am. **41**:204, 1930; Pan-Am. Geol. **53**:159, 1930.

Revised Definition.—Anticipating somewhat the data to be given, this working definition of *Aulopora* as it now stands may be offered:

Colony consisting of small tubes; adnate, prostrate, or prostrate basally with erect or more probably pendant compound branches. Reproduction by basal or lateral gemmation. Tubes calcareous or perhaps even chitinous, the former predominating; their walls non-cystose, smooth to wrinkled externally, smooth or pustulose internally. Tabulae (or diaphragms), when present, variably convex toward the apertures. Tubes not continuously united, except in rare instances in which calcification is incomplete.

Aulopora serpens Goldfuss

Aulopora serpens Goldfuss, Petref. Germ. 1:82, pl. 29, figs. 1a, b, d, 1826. (Probably *not* fig. 1c.)

Not Aulopora serpens of Rominger, Grabau and most other American authors.

Original Description.—

Aulopora incrustans, repens, tubulis strictis ex apicis latere proliferis, alternis vel in reticulum connexis, ostiolis coarctatis ascendentibus.

Die verkehrtkegelförmigen, geraden Röhrchen proliferiren nahe am obern Ende, und zwar unterhalb ihrer, nach der obern Seite übergebogenen, kreisrunden, etwas verengten Mündung. Entweder sprosset immer nur ein Röhrchen aus dem vorhergehenden aus, oder es treten zwei derselben hervor, welche sich dann gabelförmig von einander entfernen, und sich häufig wieder durch neues Aussprossen netzförmig verbinden, und Netzmaschen von verschiedener Gestalt und Grösse darstellen.

Revised Definition.—Colonies prostrate, attached to corals, and other massive organisms. Tubes uniserial, reticulate or massed so closely as to incrust the surface of the host, both reticulate and incrusting phases being found in a single colony. Tubes thick, variable in both length and diameter; in the hypotypes, the latter ranges from 1 to 2 mm. and the former from 2.4 to 4.8 mm. Apertures are round, slightly to pronouncedly constricted; a few are oblique, but most are directed vertically. Tabulae apparently rare. Reproduction chiefly by subcalycinal gemmation.

Remarks.—This species is characterized by tubes which are thick-walled in proportion to their diameter and by its pronounced polymorphism. In the larger variant, the tubes are depressed and widely expanded basally but this character does not appear in those 1 to 1.4 mm. in diameter. Hypotypes include nothing that corresponds to Goldfuss' Fig. 1c, which seems to represent a distinct species.

Though commonly identified from Hamilton and other middle to upper Devonian formations of North America, *Aulopora serpens* seems not to occur in them and most of the specimens referred to it and examined in this study belong to *Ceratopora* or *Syringopora*. Its closest American relative seems to be *A. iowensis* Hall, of the upper Devonian Hackberry formation. This species seems to be *A. serpens* minus most of its polymorphy, thickness of tubes and tendency to incrust, plus considerable elevation of both tubes and apertures, and probably may be accepted as an American descendant of Goldfuss' species.

Hypotypes.—17317-17319 Univ. Michigan.

III. Confusion of Ceratopora with Aulopora

Externally, prostrate coralla of several species belonging to *Ceratopora* Grabau[4] are very like large species of *Aulopora,* and this similarity (in the absence of sections) has led to the reference of several species of *Ceratopora* to *Aulopora.* Thus *Aulopora maxima* Fenton and Fenton[5] proves to be a *Ceratopora* with typically cystose walls. Rominger figured[6] as *Aulopora serpens* Goldfuss the prostrate tubes of a reticulate *Ceratopora,* and another species seems to have formed the basis of *Aulopora serpens* (?) of Stewart.[7]

Such American identifications of *Aulopora tubaeformis* Goldfuss as we have been able to check also are based on members of the genus *Ceratopora,* or upon *Syringoporae. A. tubaeformis* of Grabau,[8] in the Hamilton of western New York, is a *Ceratopora,* apparently undescribed. Goldfuss' illustrations, of which two are reproduced on Plate 5 Figs. 4-5, suggest that *A. tubaeformis* itself may be a *Ceratopora.*

Such examples need not be multiplied. They show the laxity with which the name *Aulopora* has been applied, and that some of its most aberrant members may be removed without reference to the problem of bryozoan-coralline convergence. Nor is it involved in the separation of a new, definitely coralline genus, *Aulocaulis.*

IV. Aulopora Compared with Stomatopora and Hederella

As has been said, many species referred to *Aulopora* show marked resemblances to such cyclostomate bryozoans as *Stomatopora* and *Hederella.* In mode of growth and type of reproduction there is a very close similarity between certain forms of *Stomatopora* and *Aulopora;* their only substantial difference appears to be size. Thus *Stomatopora dichotoma* Lamouroux is very nearly a miniature of *Aulopora saxivadens* Hall and Whitfield,[9] as the familiar enlargement in Zittel-Eastman[10] well shows. *Aulopora minima* Fenton and Fenton[11] shows the same resemblance. In size it is a *Stomatopora,* and has been so considered by one competent worker; yet in manner of growth and character of tubes it strikingly resembles the much larger *Aulopora delicata* M. A. Fenton,[12] which is almost a contemporary.

The geologic ranges of *Stomatopora* and *Aulopora* suggest that some species assigned the latter really belong to the former genus. The range of *Stomatopora* is given as Ordovician, Jurassic, Cretaceous, Tertiary and Recent,

4 Proc. Boston Soc. Nat. Hist. **28**:414, 1899; Bull. Buffalo Soc. Nat. Sci. **6**:132, 1899.
5 Stratig. and Fauna of the Hackberry Stage of the Upper Devonian: 66, pl. 16, fig. 7, 1924.
6 Geol. Surv. Mich. **3**(2):87, pl. 33, fig. 2, 1876.
7 Geol. Surv. Ohio (4), Bull. **32**: 19, pl. 1, fig. 4, 1927.
8 Bull. Buffalo Soc. Nat. Sci. **6**:132, fig. 16, 1899.
9 Ann. Rep. N. Y. State Mus. **23**:235, pl. 10, fig. 6, 1873.
10 Text-book of Paleontology **1**:319, 1913.
11 Stratig. and Fauna of the Hackberry Stage of the Upper Devonian: 69, pl. 16, figs. 5-6, 1924.
12 This Journal: **10**:381, pl. 1, figs. 2-4, 1927.

while *Aulopora* is chiefly Devonian and Carboniferous, with a few Silurian species. If the two ranges are combined, we get one which, though still broken, presents a less serious gap than does that of *Stomatopora* alone.

Though *Hederella* is less like *Aulopora* than is *Stomatopora,* the fact that they are common in the same formations makes their similarities more noticeable. The diagnostic character of *Hederella* is that of a central axis from which tubes are given off. This same character has been observed in one of the many variations of *Aulopora aperta* Winchell (Plate 2, Fig. 6), and in *A. confluens* M. A. Fenton (Plate 2, Fig. 3). Tabulae—or diaphragms—are common in both genera.

Even the massed, incrusting manner of growth found in *Aulopora conferta* Winchell has its counterpart in the smaller genus, of a supposedly different phylum. Thus two specimens of *Hederella,* one of which is shown in Text Figure 1, have their tubes so closely grouped together that they present an appearance very like such incrusting forms of *Aulopora* as *A. munda*[13] and *A. conferta* (Plate 1, Fig. 4). *Hederella* is distinct enough when its characters are ideally represented, but when it has deviated from this ideal—and prostrate forms are noted for their variability—its appearance is so very like some species of *Aulopora* as to suggest that some of its larger members now masquerade as corals.

V. Comparison of Aulopora and Plumatella

Plumatella, a modern fresh water bryozoan of the order *Phylactolaemata,* has growth habits like those of some Auloporoids. Zoaria attach themselves to foreign objects such as rocks, logs and even cornstalks, in such a way as to present an appearance very like that of supposedly typical *Auloporae.* A comparison of Figures 6 and 7 of Plate 3 will show such a similarity; when the tubes of Plumatella (Plate 1, Fig. 1) grow so close together as practically to incrust the surface of the foreign object they look like the *Aulopora* of Figures

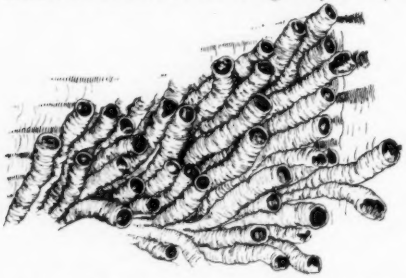


Fig. 1. A *Hederella,* perhaps *H. canadensis* (Nicholson), from the Traverse (Gravel Point) of Michigan, showing an incrusting type of growth similar to that of *Aulopora conferta* Winchell, (Plate 1, Figs. 3-4.) x 6.

2 and 3 of Plate 1. It is usually in swift flowing streams that the zoaria take this form of growth, for in quiet waters *Plumatella* has sufficient attachment to foreign objects to support the zoarium, and the remaining tubes, reproducing in the usual manner, hang downward. Figure 1, Plate 2, shows such a

13 This Journal **10**:377, pl. 2, fig. 15, 1927.

colony; it is here, however, reversed in order that the illustration may conform to a convention long established for the genus *Aulopora.*[14] The first suggestion that pendant colonies of *Plumatella* might aid in explaining certain peculiar Auloporoid zoaria came from the study of the unusual form from the Hackberry Stage which the senior author has called *Aulopora confluens.*[15] What seems to be the basal attachment, in one case, adheres to the surface of a branching bryozoan, (Plate 2, Figs. 4-5), while the massed columns of tubes, (Plate 2, Figs. 2-3), closely resemble the pendant portion of a *Plumatella* colony, (Plate 2, Fig. 1), and probably hung downward in a similar manner. The column, of course, might have grown upward; but in a similar form from the Traverse of Michigan, *Aulopora aperta* Winchell, the basal attachments were on the under surfaces of objects such as *Prismatophyllum,* (Plate 2, Fig. 7), and the columns, (Plate 2, Fig. 9 and Plate 3, Figs. 3 and 5), must have extended downward. This latter point brings up the type of the material of the walls. In the fresh water form, *Plumatella,* the walls are chitinous and the appearance of some specimens of *Aulopora aperta* Winchell suggests that they may have shared this character. Not merely are the tubes thin; they are collapsed and apparently shrunken in a manner resembling the dried *Plumatella princeps* of Plate 3, Fig. 7. To a lesser degree, the delicate tubes of *Aulopora confluens* M. A. Fenton also show these characters.

This is a possibility suggested by selected specimens; others—a majority—indicate calcareous tubes whose walls were much thinner in proportion to size than were those of *Hederella, Stomatopora, Hernodia* or *Reptaria.* As a rule, thin-walled species show closer resemblance to admitted bryozoans than do the thick-walled types, most of which are definitely coralline.[16]

In still two other characters *Aulopora* and *Plumatella* are similar. In a thin section of *Plumatella,* (Plate 4, Fig. 6), is a diaphragm that compares very closely with "tabulae" in the section of *A. michiganensis,* (Plate 4, Fig. 7). Tabulae or diaphragms are not uncommon in well preserved specimens of *Aulopora* but the small size of the tubes makes it difficult to prepare sections suitable for study. A tabula or diaphragm is also shown on Plate 3, Fig. 2. The *Aulopora* tabulae shown here, as well as all others seen, are like diaphragms of *Plumatella:* the convexity is toward the opening of the tube.

Finally, some Auloporoids show continuity of tubes, which seems to imply the continuous connection of body cavities which characterizes the Phylactolaematous bryozoans. As seen in *A. aperta* Winchell (Plate 3, Fig. 2) this appears as partial constriction of some tubes whose associates preserve the apparently normal, distinct character.

VI. Conclusions

To us it seems clear that *Aulopora,* even with members of *Ceratopora* and other genera removed, includes members of both "tabulate" (Alcyonarian)

14 Goldfuss, Petref. Germ. **1**:82-84, pl. 29, figs. 1-4 and pl. 38, fig. 17, 1826.

15 This Journal **10**:380, pl. 2, figs. 1-7, 1927.

16 Calcareous walls in Auloporoids do not invalidate comparisons with *Plumatella.* If the latter is a relict marine genus that has taken refuge in fresh water, its chitinous walls may be secondary, through loss of the calcareous character.

corals and bryozoa, the latter chiefly of the order Hederelloidea Bassler.[17] Since the genotype is a coral, the bryozoans ultimately must be assigned to genera within their own order. For only two such species, *A. (= Stomatopora) minima* of the Hackberry formation and *A. (= Hederella) serpuloides* of the Traverse, are we prepared to make assignment with assurance. Pending further study, therefore, it seems best to use *Aulopora* as a form-genus including members of *Aulopora* proper, undetermined corals and bryozoans. The following list indicates the relationships of species in the American Devonian and others described by Goldfuss:

"TABULATA" (Alcyonaria)

Aulopora Goldfuss, *sensu stricto*.

A. belanskii Fenton and Fenton,[18] Shellrock, Iowa
A. iowensis Hall and Whitfield, Hackberry, Iowa
A. irregularis M. A. Fenton, Shellrock, Iowa
A. modulata M. A. Fenton, Shellrock, Iowa
A. jugalis M. A. Fenton, Shellrock, Iowa
A. multiramosa M. A. Fenton, Shellrock, Iowa
A. munda M. A. Fenton, Shellrock, Iowa
A. norensis M. A. Fenton, Shellrock, Iowa
A. saxivadens Hall and Whitfield, Hackberry, Iowa
A. scohariae Hall, Lower Helderberg, New York
A. serpens Goldfuss, Crinoidenschichten, Eiffel
A. stainbrooki M. A. Fenton, Shellrock, Iowa

Aulocaulis Fenton & Fenton, gen. nov.[19]

A. annectens (Clarke) Lower Naples, New York
A. expansus Fenton and Fenton, Hackberry, Iowa
A. linearis M. A. Fenton, Shellrock, Iowa

Ceratopora Grabau.

Aulopora maxima Fenton and Fenton, Hackberry, Iowa (= *Ceratopora maxima*)[20]
"*A. tubaeformis* Goldfuss," Grabau, Hamilton, New York
"*A. serpens* Goldfuss" Rominger, Traverse, Michigan

Generic relationship uncertain; probably within the *Moniloporoidae and Syringoporoidae*.

Aulopora conglomerata Goldfuss, Crinoidenschichten, Eiffel
A. elongata Hall, Helderberg, New York
A. erecta Rominger, Traverse, Michigan
A. schucherti Swartz, Helderberg, Maryland
A. subtenuis Hall, Helderberg, New York
A. tubaeformis Goldfuss, Uebergangskalke, Eiffel
A. tubula Hall, Helderberg, New York

BRYOZOA, order HEDERELLOIDEA Bassler

Aulopora adnascens Fenton and Fenton, Hackberry, Iowa
A. aperta Winchell, Traverse, Michigan

---

17 Proc. Geol. Soc. Am. **1934**:346, 1934.
18 New name, to replace *A. elongata* M. A. Fenton, this Journal **10**:380, pl. 1, fig. 11, 1927; preoccupied by *A. elongata* Hall, Ann. Rep. N. Y. State Mus. **32**:143, 1879.
19 This Journal **18**(1):119, 1937.
20 New generic assignment.

A. conferta Winchell, Traverse, Michigan
A. confluens M. A. Fenton, Hackberry, Iowa
A. crebriformis M. A. Fenton, Shellrock, Iowa
A. cyclopora Winchell (= *A. conferta* Winchell or is invalid) Traverse, Mich.
A. delicata M. A. Fenton, Shellrock, Iowa
A. incrustans Fenton and Fenton, Hackberry, Iowa
A. minima Fenton and Fenton, Hackberry, Iowa *(Stomatopora minima)*[21]
A. paucitubulata Fenton and Fenton, Hackberry, Iowa *(Stomatopora? paucitubulata)*[21]
A. serpuloides Winchell, Traverse, Michigan *(Hederella serpuloides)*[21]

ANNELIDS (?)

A. cornulites Hall, Helderberg, New York. (A species not determinable from illustrations; types have not been traced.)

21 New generic assignment.

Species of Aulopora from the Traverse and Hamilton Groups

Mildred Adams Fenton

I. Introduction; Acknowledgments

Seventy years ago, Alexander Winchell described[1] without illustrations a number of fossils from the Devonian Traverse group of Michigan, four species being assigned to *Aulopora*. One of these, *A. serpuloides*, is determinable, even from the scanty description, as bryozoan, probably *Hederella*. Another, *A. conferta*, was redescribed and figured by Rominger;[2] the others, though listed by Pohl[3] in his paper on Traverse stratigraphy, remained unidentifiable. Since types were known to exist, they prevented further description of the abundant and excellently preserved Traverse Auloporoids.

The present study was begun on specimens loaned by Mr. A. W. Slocom, of the University of Chicago, and was continued on specimens collected for the University of Cincinnati in 1926. It has been completed after examination of Winchell types and of specimens in the Museum of Paleontology of the University of Michigan, lent by Dr. G. M. Ehlers. To these have been added specimens of an apparently new species from the Hamilton of western New York, collected by Mr. E. R. Eller, of the Carnegie Museum. This final work, like completion of the preceding paper, was made possible by a grant from Elizabeth Thompson Science Fund.

1 The Grand Traverse Region. A Report of the Geological and Industrial Resources of the counties of Antrim, Grand Traverse, Benzie and Leelanau in the Lower Peninsula of Michigan: 91-92, 1866.

2 Geol. Surv. Mich. **3**(2):88, pl. 33. fig. 1, 1876.

3 Proc. U. S. Nat. Mus. **76**:(14) no. 2811, 1930.

II. Descriptions

Aulopora aperta Winchell

Pl. 2, Figs. 6-9; Pl. 3, Figs. 1-5.

Aulopora aperta Winchell, The Grand Traverse Region, etc.: 91, 1866.

Description.—Colonies are attached to surfaces of stromatoporoids, corals, several species of bryozoans and brachiopods. Not infrequently columns are formed by the piling up of the tubes; Plate 2, Fig. 8 shows the beginning of two such columns, and Plate 2, Fig. 9 shows an incomplete specimen measuring 26.7 mm. in length and 6.6 mm. in diameter. Three specimens, one of which is represented on Plate 3, Fig. 3, show that branching of the columns themselves occurred. A cross section of such a column, Plate 3, Fig. 1, shows that the walls are distinct and comparatively heavy; the longitudinal section, Plate 3, Fig. 2, shows the way in which the columns are formed. The readiness with which the tubes separate indicates that the wall of each tube is distinct. There are indications of diaphragms, one at the point marked d. Growth appears to be by basal gemmation within the columns.

Adnate portions of this species grow very irregularly, as is shown on Plate 2, Fig. 7. The method of reproduction is by both basal and lateral gemmation, though the latter appears to be the more common. Not infrequently two or more, and in one case five, tubes are given off laterally from the parent tube. The lengths of the tubes vary so much that measurements are meaningless.

Remarks.—A small form, Plate 3, Figs. 4-5, is found associated with the typical *A. aperta* Winchell: for the present, at least I consider the two forms together, calling attention to the difference in size—the only distinctive character. The variation in both size and type of growth is very noticeable among the fifty-odd specimens at hand.

Determination of the species is based upon Winchell's holotype, shown in Text Fig. 1; though very poor, with tubes largely worn away, it suffices for identification of the many good specimens now available.

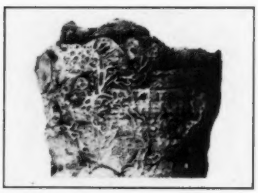


Fig. 1. Holotype of *Aulopora aperta* Winchell, x 1. Bell Quarry, SW quarter Sec. 2, T43N, R6W, Emmet County, Mich. 14304A Univ. Mich.

Occurrence.—Gravel Point Stage, Zone 6, bed 1 or possibly Zone 4, bed 3 of Pohl, Bell Quarry, Emmet Co., Michigan.

Holotype.—14304A Univ. Michigan; *Hypotypes.*—1400-1406 and 1436-1437 Univ. Cincinnati Museum; 25975 Walker Museum.

Aulopora cyclopora Winchell, invalid

Aulopora cyclopora Winchell, The Grand Traverse Region, etc.: 92, 1866.

Remarks.—Winchell's unpublished figure shows a small colony of *Aulopora* whose tubes have the expansion and apertural constriction of *A. conferta.* It closely resembles the *A. conferta* of Plate 3, Fig. 6. In the Alma College museum, however, is a specimen numbered 2711 and recorded as *A. cyclopora* by Winchell; the number is immediately adjacent to a typical colony of *A. aperta* in which the tubes do not anastomose, thus corresponding to Winchell's description. They also show lengths equal to those given (2.29-3.56 mm.) and apertures of similar diameter.

Since the holotype, from which Winchell's drawing was made, has not been found, the species cannot be recognized. It appears to be a synonym of *A. conferta* or *A. aperta.*

Aulopora conferta Winchell

Pl. 1, Figs. 2-5; Pl. 3, Fig. 6.

Aulopora conferta Winchell, The Grand Traverse Region, etc.: 91, 1866.

Aulopora conferta Rominger, Geol. Surv. Michigan **3**(2):88, pl. 33, fig. 1, 1876.

Description.—Colony attached to surfaces of stromatoporoids and corals. Tubes typically grouped so closely together as to incrust the host, Plate 1, Figs. 2-4, though in a few cases they are arranged uniserially, Plate 3, Fig. 6. The tubes vary considerably in size, as is shown by the figures. Measurements of three typical tubes, the first from an incrusting mass, the second and third from uniserial colonies, the last representing a slightly larger form of the species: length 1.5, 2 and 3.3 mm.; diameter at point of origin: 0.7, 0.7 and 1.2 mm.; maximum diameter 1.3, 1.1 and 1.3 mm.

Apertures are round, rising slightly above the general surface of the colonies; where massed, 4 are found in the space of 5 mm. Lateral gemmation occurs though basal is the more common; from one to three tubes arise from each parent. Surfaces bear fine transverse wrinkles.

Remarks.—This species closely resembles *Aulopora jugalis* M. A. Fenton[6] from the Shellrock of Iowa but differs from it in having smaller tubes and a less coarse appearance.

Occurrence.—Gravel Point Stage, Zone 6, bed 1 or possibly Zone 4, bed 3 of Pohl, Bell Quarry, Emmet Co., Michigan.

Cotypes.—14301 Univ. Michigan; *Hypotypes.*—1407-1408 Univ. Cincinnati Museum and 25973 and 25978 Walker Museum.

Aulopora socialis sp. nov.

Pl. 4, Figs. 1-5.

Description.—Colonies incrusting corals, bryozoans and brachiopods.

6 This Journal **10**:378, 1927.

Walls of the tubes coalesce so that the surface of the host is completely obscured; the tubes are comparatively short and the walls are heavy. Apertures, where well preserved, are round and oblique.

The unique character of this species is the spines on the inner walls of the tubes; they are most conspicuous on weathered specimens such as the one shown in Plate 4, Fig. 2. Enlargements (Plate 4, Figs. 3 and 4) show the arrangement of these spines. The median spines, arranged in imperfect rows (Plate 4, Fig. 1), appear to be heavier than those on other parts of the wall. One diaphragm was noted.

Remarks.—This species has a mode of growth similar to that of *Aulopora conferta* Winchell, but differs from it in having coarse tubes and heavy, spinose walls.

Occurrence.—Gravel Point Stage, Zone 6, Bell Quarry, Emmet Co., Michigan.

Holotype.—1411; *Paratypes.*—1412-1413 Univ. Cincinnati Museum.

Aulopora michiganensis sp. nov.

Pl. 4, Figs. 7-8.

Description.—Colonies commonly attached to surfaces of stromatoporoids and corals; over smooth surfaces the growth is regular, but on rough ones it is irregular, with tubes commonly growing over each other. Tubes comparatively heavy; typically, they are small at the point of origin, with uniform expansion anteriorly. At the place where each tube turns upward two new ones generally are given off; this gives a false appearance of abrupt increase in diameter. Apertures are round and rise well above the general surface of the tubes.

Dimensions of a typical tube of the holotype are: length 3.2 mm.; minimum diameter 1.6 mm.; maximum diameter 1.9 mm.; height of aperture above base of tube 2.3 mm.; diameter of aperture 1.1 mm. Diaphragms (or tabulae) not commonly preserved; two are shown on Plate 4, Fig. 7.

Occurrence.—Gravel Point Stage, Zone 6, Bell Quarry, Emmet Co., Michigan.

Holotype.—1409; *Paratypes.*—1410 Univ. Cincinnati Museum, and 25974 Walker Museum.

Aulopora elleri sp. nov.

Aulopora serpens Goldf., Grabau, Buffalo Soc. Nat. Sci. Bull. **6**:132, fig. 15, 1899.

Description.—Colony (corallum) prostrate, attached throughout, loosely reticulate. Branching occurs every second or third tube, the branching tubes forming angles of 80 or more degrees. Tubes expand moderately except in the terminal region, where they enlarge abruptly in some cases and definitely in all. Walls thick; they are smooth externally or bear indistinct, rounded wrinkles. Apertures subellipsoidal, oblique or vertical, not constricted. No

tabulae seen. Dimensions of three tubes: length 6.2, 6.3 and 6.4 mm.; diameter at point of origin 0.8, 1.0 and 0.8 mm.; maximum diameter 2.3, 2.4 and 2.2 mm.

Remarks.—This species seems closely related to *Aulopora scohariae* Hall of the Helderberg, from which it differs in having larger and longer tubes, more ellipsoidal and less elevated apertures and less distinct growth ridges. Its tubes also are less distinct at the point of branching.

Occurrence.—Hamilton (Moscow), Little Beard Creek near Leicester (= Moscow) and other localities in western New York.

Holotype.—7418; *Paratype.*—7419 Carnegie Museum.

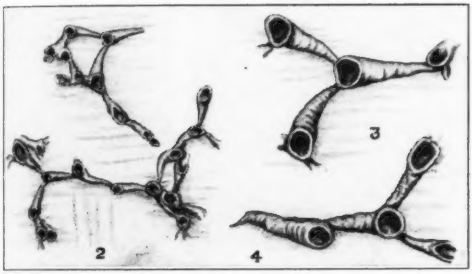


Fig. 2. *Aulopora elleri* sp. nov. Holotype, x 1.

Figs. 3-4. Same; details of branching, x 2. Hamilton (Moscow), Little Beard Creek near Leicester, N. Y.

Aulocaulis, a New Genus of Auloporoid Corals

Mildred Adams Fenton and Carroll Lane Fenton

In preparing our paper on the form-genus *Aulopora,* we encountered several species which, though they seem to be corals, differ markedly from Goldfuss' genus and from others *(Syringopora, Romingeria, Ceratopora)* commonly confused with it. It seems proper, therefore, that they form the basis of a new genus of the family Auloporidae.

Aulocaulis gen. nov.

αυλός, tube; καυλός, stem

Genoholotype: *Aulopora expansa* Fenton and Fenton. Genoparatype: *A. linearis* M. A. Fenton.

Description.—Corallum prostrate, linear or reticulate. Corallites thin-walled, depressed, smooth or indistinctly wrinkled. Throughout most of their length they show little or no expansion; then they expand abruptly into sub-

circular apertural regions whose diameter is 1.5 to 4 times that of the tubular portions of the corallites. The apertures are directed vertically and are but slightly elevated above the tubes. Tabulae few or absent; septal ridges present. Some species bear an indistinct dorsal ridge on most or all corallites.

So far as growth lines indicate, the aperture is nearly horizontal in early stages, before development of the enlarged portion. Growth, however, must have been rapid for no corallites in this stage have been observed. Reproduction chiefly by terminal budding; branching or in linear series.

Remarks.—The following species, all described as *Auloporae,* are referred to this genus:

Aulocaulis expansus (Fenton and Fenton), Stratig. and Fauna of the Hackberry Stage of the Upper Devonian: 67, pl. 16, fig. 10, 1924. Devonian (Hackberry), Iowa.

Aulocaulis annectens (Clarke), U. S. Geol. Surv., Bull. 16: 63, fig. 15, 1885. Devonian (Naples Beds), New York.

Aulocaulis linearis (M. A. Fenton), Am. Midl. Nat. 10: 379, pl. 1, fig. 10, 1927. Devonian (Shellrock), Iowa.

Aulocaulis sp. indet. Devonian (Cedar Valley) near Brandon, Iowa. Available specimens are too poorly preserved for description, but show a species more like *Aulopora* than are the three just mentioned.

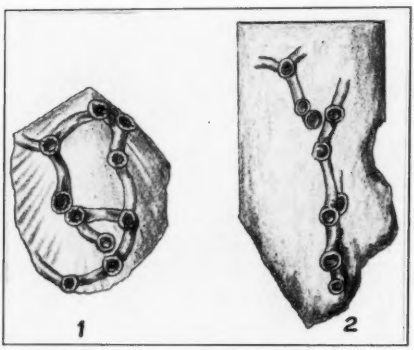


Fig. 1. *Aulocaulis annectens* (Clarke). The holotype, x 1. (14976 U. S. National Museum.)

Fig. 2. *Aulocaulis expansus* (Fenton and Fenton). The holotype, x 1. (26021 Walker Museum.)

Aulopora procumbens Davis (Kentucky Fossil Corals 2: pl. 73, figs. 12-13) has the depressed, prostrate tubes characteristic of *Aulocaulis*. Dr. V. J. Okulitch has examined the types and reports that they show both funnels and cysts in the vertical, expanded parts of the tubes. This links the species with *Ceratopora dichotoma* Grabau, from which it differs in being attached along the entire surface. It clearly is not referable to *Aulocaulis*.

PLATE 1

FIGURES

1. *Plumatella princeps* Kraepelin. A fresh water bryozoan almost incrusting a rock. Except for size, there is little difference between this and the *Aulopora* of Fig. 4. x 2. (G. B. Twitchell Coll.)

2–5. *Aulopora conferta* Winchell.

2. A typical colony attached to a cyathophylloid coral, x 2. (1414 Univ. Cincinnati Museum.)

3. A similar colony on the under surface of a *Prismatophyllum*, x 1. (25978 Walker Museum.)

4. An example of the fan-shaped type of growth is shown in the upper part of this figure, and of the irregular massing of tubes in the lower. x 1. (1415 Univ. Cincinnati Museum.)

5. A less common growth form in which the tubes are distinct. Their origins can be traced readily. x 2. (1408 Univ. Cincinnati Museum.)

PLATE 2

FIGURES

1. *Plumatella princeps* Kraepelin. A modern fresh water bryozoan. The basal part of this specimen was attached to the under surface of a rock and the portions shown here hung down and moved freely in the water. This figure, compared with Figs. 2 and 3, suggests the mode of growth of similar fossil forms x 2. (G. B. Twitchell Coll.)

2–5. *Aulopora confluens* M. A. Fenton.

2–3. Two views of a specimen showing growth similar to that of *Plumatella*, Fig. 1. In this *Aulopora* the tubes grew upon each other while in *Plumatella* the zooecia are not cemented together. x 2. (C. H. Belanski Coll.)

4–5. Two views of what appears to be the basal attachment of columns such as are shown in Figs. 2 and 3. x 2. (2036 Univ. Cincinnati Museum.)

6–9. *Aulopora aperta* Winchell.

6. A colony in which tubes arise by both basal and lateral gemmation. x 2. (1406 Univ. Cincinnati Museum.)

7. A colony attached to the under surface of a *Prismatophyllum*. Near the center tubes grow over each other in such a way as to suggest the beginning of columns, an example of which is shown in Fig. 9. x 1. (1400 Univ. Cincinnati Museum.)

8. Tubes grown over each other so as to form the bases of columns. x 2. (1402 Univ. Cincinnati Museum.)

9. A portion of a column composed of distinct tubes growing upon each other. It probably was attached to the under surface of a coral and hung downward. x 2. (1401 Univ. Cincinnati Museum.)

PLATE 3

FIGURES

1–5. *Aulopora aperta* Winchell.

1–2. Cross and longitudinal sections of a column such as is shown on Plate 2, Fig. 9, showing the comparatively heavy, distinct walls. At the point d in Fig. 2 there is an indication of a diaphragm: the heavier structure above d is the wall and this, as well as similar ones, should not be mistaken for diaphragms. x 10. (1404 and 1403 Univ. Cincinnati Museum.)

3. A column showing three divisions or branches. x 1. (1405 Univ. Cincinnati Museum.)

4. A colony composed of small tubes. x 1. (1436 Univ. Cincinnati Museum.)

5. A column made up of small tubes. x 2. (1437 Univ. Cincinnati Museum.)

6. *Aulopora conferta* Winchell. A colony deviating from the usual incrusting form of growth characteristic of this species. These uniserial tubes have a mode of growth similar to that of the *Plumatella* shown in Fig. 7. x 1. (1407 Univ. Cincinnati Museum.)
7. *Plumatella princeps* Kraepelin. A fresh water bryozoan that closely resembles an *Aulopora* in type of growth. x 2. (G. B. Twitchell Coll.)

PLATE 4

FIGURES

1–5. *Aulopora socialis* n. sp.
1. A thin section from the holotype showing spines on the inner walls of the tubes. x 10. (1411 Univ. Cincinnati Museum.)
2. A colony incrusting the surface of a fragmentary *Spirifer*. Spines can be seen in several tubes. x 2. (1412 Univ. Cincinnati Museum.)

3–4. Enlarged views of several tubes showing the spines of the inner wall. x 10. (1412 Univ. Cincinnati Museum.)

5. Holotype showing the mode of growth. x 2. (1411 Univ. Cincinnati Museum.)
6. *Plumatella princeps* Kraepelin. A thin section of a freshwater bryozoan possessing a diaphragm. Compare this section with the one shown in Fig. 7. x 10. (G. B. Twitchell Coll.)

7–8. *Aulopora michiganensis* n. sp.
7. A thin section of a tube of the holotype. Two definite diaphragms are present. x 10. (1409 Univ. Cincinnati Museum.)
8. Holotype attached to the surface of a stromatoporoid. x 1. (1409 Univ. Cincinnati Museum.)

PLATE 6

FIGURES

1. *Aulopora multiramosa* M. A. Fenton. Holotype: the tubes are coralline. x 1. (870 Belanski Coll.)

2–4. "*Aulopora*" *delicata* M. A. Fenton.
2. The holotype, x 1. (2033 Univ. Cincinnati Museum.)
3. Enlargement of the first three tubes, x 8. They suggest very thin calcareous tubes of bryozoans.
4. The holotype, x 2.

5–9. *Aulopora modulata* M. A. Fenton.
5. The holotype, showing coralline tubes. x 1. (1045 Belanski Coll.)

6–7. A paratype also with strong tubes, and enlargement of same to show apertures. x 1 and x 2. (1904 Belanski Coll.)

8. Lateral view of two tubes of the same corallum. x 2.
9. A third paratype, with tubes of smaller diameter. x 1. (2060 Belanski Coll.)
10. *Aulocaulis linearis* (M. A. Fenton). The holotype, showing prostrate tubes and large, vertically directed apertures. x 1. (1943 Belanski Coll.)
11. *Aulopora belanskii* Fenton & Fenton. Holotype, x 1. (848 Belanski Coll.)
12. *Aulopora stainbrooki* M. A. Fenton. Holotype, showing thick coralline tubes, x 1. (6016 Belanski Coll.)

PLATE 1

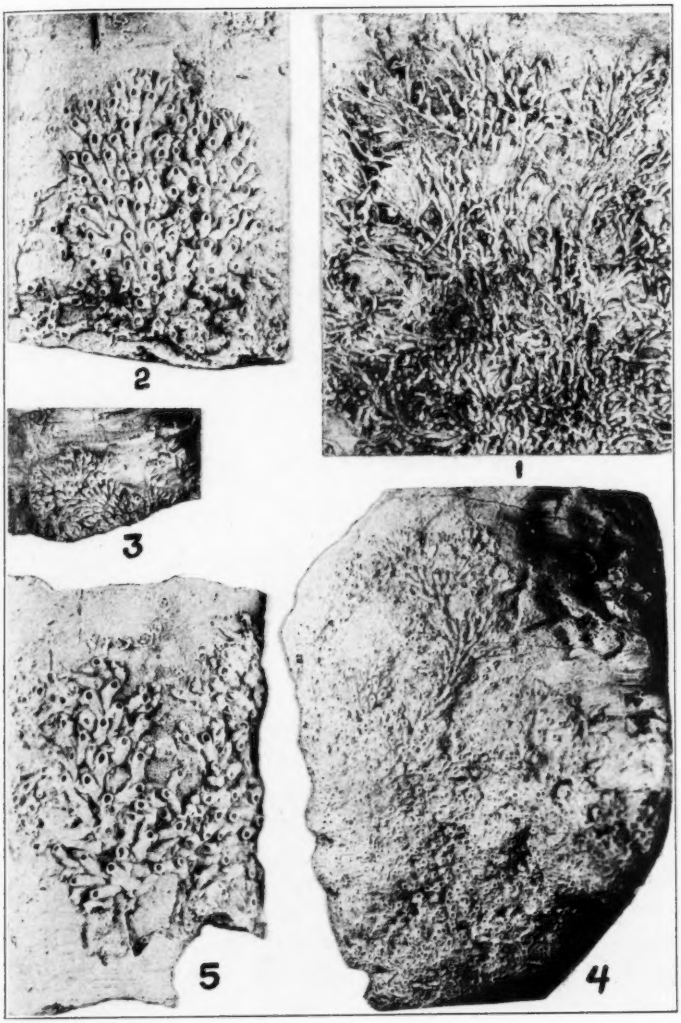


PLATE 2

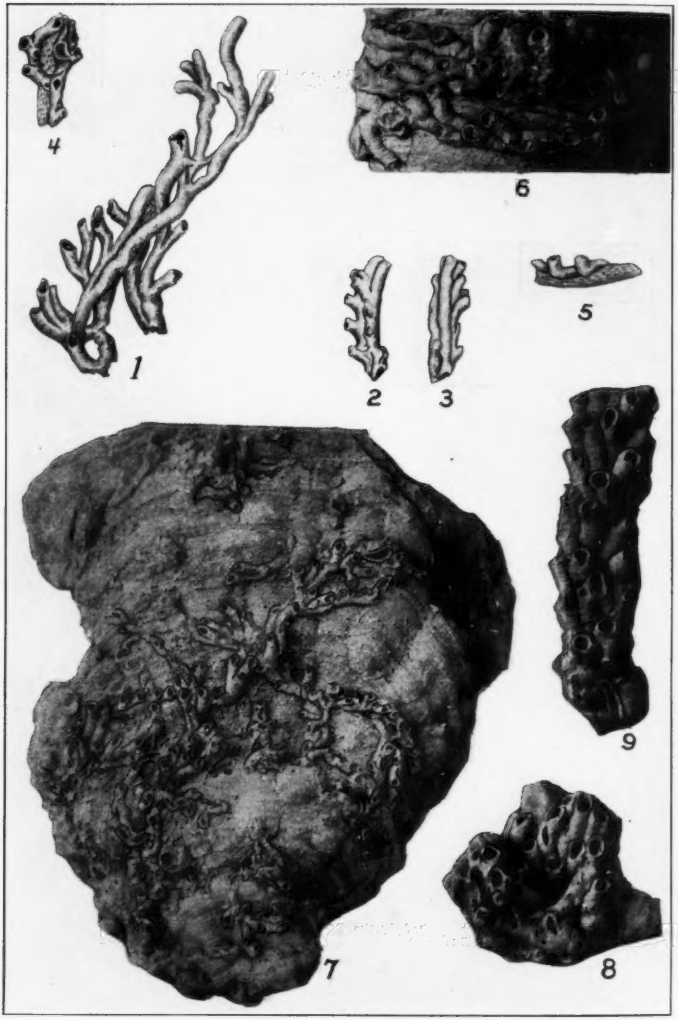


PLATE 3

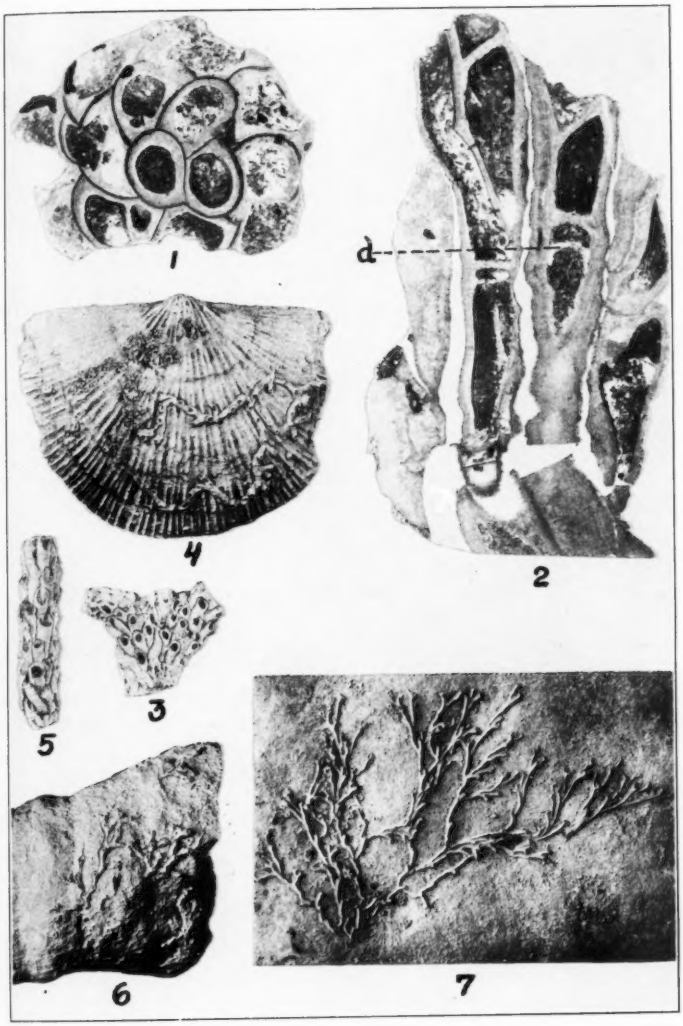


PLATE 4

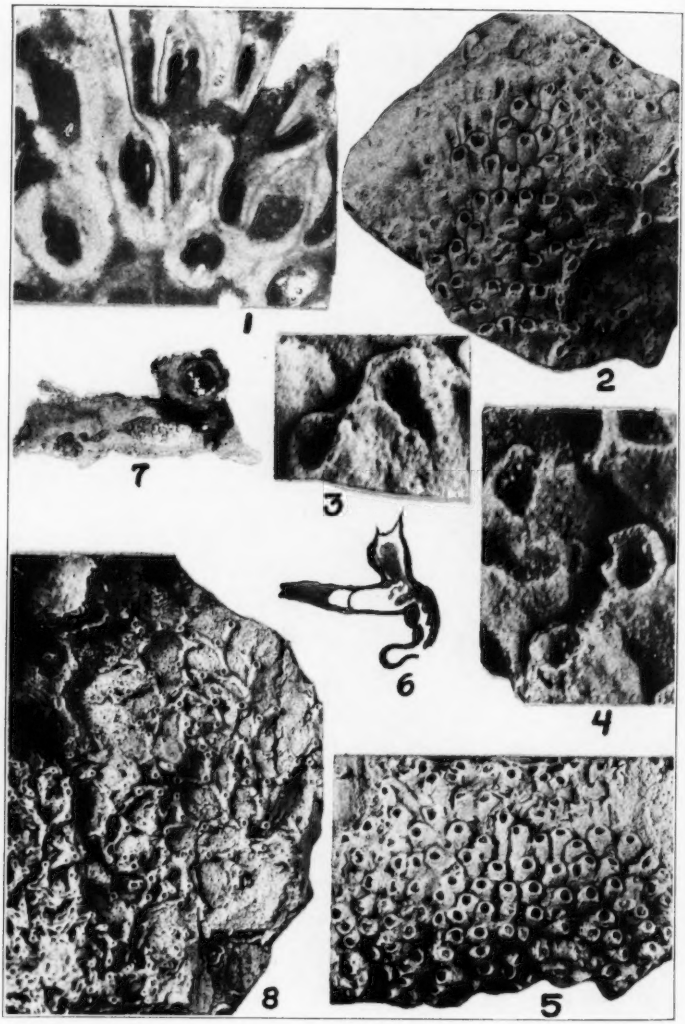
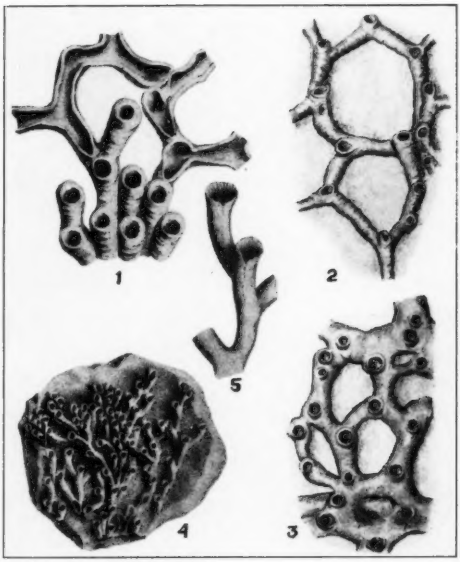


PLATE 5



FIGURES

1-3. *Aulopora serpens* Goldfuss.

1. Transverse section, enlarged, showing freedom from cysts and funnels such as characterize *Ceratopora* Grabau. After Goldfuss.

2. Widely spaced tubes of average thickness. Crinoidenschichten, Eiffel. (17317 Univ. Michigan.)

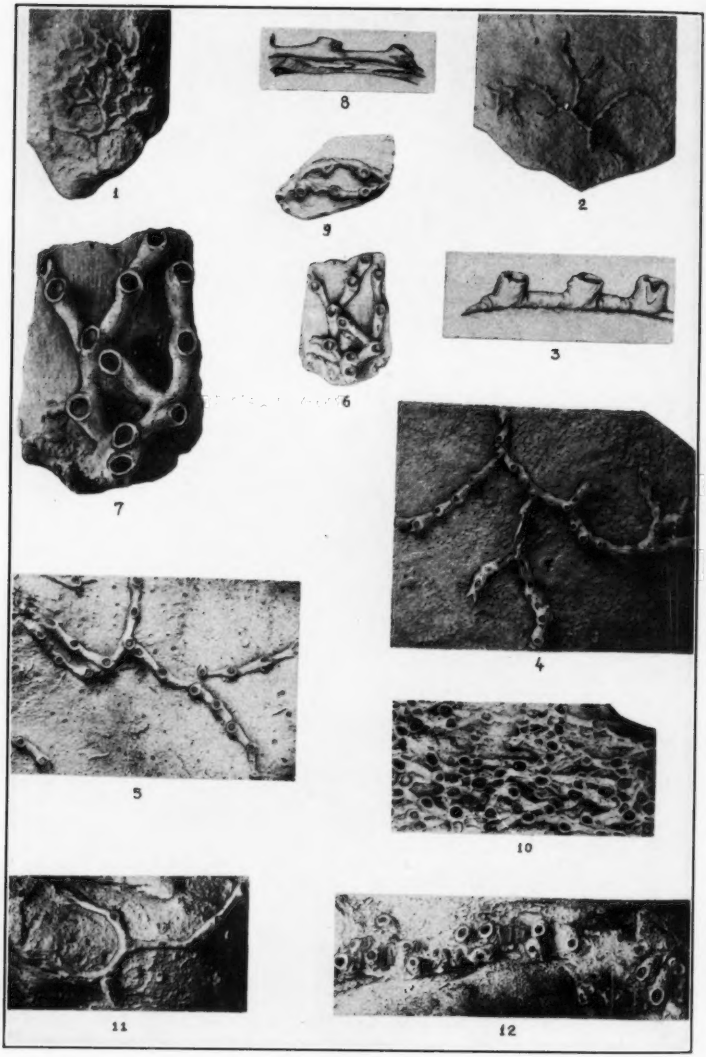
3. Closely spaced tubes with very thick walls in which secondary deposits partly obscure branching. Crinoidenschichten, Eiffel. (17318 Univ. Michigan.)

4-5. *Aulopora tubaeformis* Goldfuss.

4. Branching colony showing the partly attached tubes. After Goldfuss. x 0.5.

5. Two tubes, enlarged, showing septal ridges or rows of cysts. After Goldfuss.

PLATE 6



Mid-Tertiary Vertebrates from the Texas Coastal Plain: Fact and Fable

Horace Elmer Wood, 2nd., and Albert Elmer Wood

Fragmentary fossil mammals of Middle Miocene to Lower Pliocene aspect have been reported from a dozen localities in the Oakville and equivalent and overlying formations of the Texas Coastal Plain.[1] Deussen (1924) described a rhinoceros maxilla[2] (U.S.N.M. No. 6573, Figs. 4a and 4b) from the Derrick Farm, Washington County, Texas, supposedly from the base of the Oakville. Gidley (in Deussen, 1924) referred the Derrick Farm specimen to *"Coenopus," sensu lato,* considering it of late Miocene aspect. Re-study assigned it to *Caenopus, sensu strictiore,* known only from the Oligocene (see below), so that a reinvestigation of the locality seemed highly desirable. Weeks (1933, p. 456) regarded the locality at which this jaw was found as Catahoula, which formation is usually considered to be Oligocene, a determination which agrees with the morphology of the fossil and with the field observations of the junior author.

The senior author is solely responsible for the discussion of *Caenopus*, the junior author for the local stratigraphy. The opportunity to describe the *Caenopus* maxilla and to use Figs. 4a and 4b are due to the kindness of Mr. C. W. Gilmore of the U. S. National Museum.

During the summer of 1935, the junior author, together with Mr. Theodore Venard, of Atlanta, Georgia, visited the Derrick Farm locality under the guidance of Mr. Frank Derrick, who found the *Caenopus* jaw, and his son, Mr. C. F. Derrick. The jaw was found about five miles west of Burton, Washington County, Texas (Fig. 1). Mr. Derrick kindly pointed out exactly where he had found the jaw, on Water Run, in the middle of a six or eight foot undercut bank of brown, crackly, massive shale without visible bedding (Fig. 2), which corresponds with Deussen's description of the upper part of the Catahoula Formation. There were numerous gray clay concretions in the shale, but no additional fossils were discovered here.

Before the structure and stratigraphic significance of this *Caenopus* jaw can be discussed to any purpose, it is necessary to clarify the scope and stratigraphic distribution of the genus *Caenopus*, which has been used to mean "all things to all men." Before 1878, the American Oligocene true rhinoceroses were usually called either *"Rhinoceros"* or *"Aceratherium."* Brandt (1878) proposed the subgenus or section *"Subhyracodon"* including *Aceratherium*

1 Applin (1925), Deussen (1924), Dumble (1915 and 1918), Hay (1924), Leidy (1860, 1865 and 1869), Plummer (1932), Shumard (1863) and Weeks (1933), based on determinations largely by Camp, Gidley, Gilmore, Hay, Leidy, Matthew and Stock.

2 This has nothing to do with the jaw and teeth found in a well at Old Washington (Dumble, 1918), about which nothing further has been made public.

mite Cope, *A. occidentale* Leidy and *A. quadriplicatum* Cope. *A. quadriplicatum*, a milk dentition of *A. occidentale*, was made the type of *Anchisodon* Cope, 1879; and *A. mite* was made the type of *Caenopus* Cope, 1880. Wood (1927, pp. 55 and 59) believed[3] that Matthew accepted *Subhyracodon* as valid and had fixed the type of the genus by elimination (Cope and Matthew, 1915). However, such designation must be explicit and not implicit, so that either the type species was designated by Wood (1927, pp. 54-55, 59, 68 and 72), or is still not properly chosen, in which case "*Aceratherium*" *occidentale* (Leidy) is hereby so designated.

There has been considerable objection to the use of the name "*Subhyracodon*" because of the incorrect relationship implied by the name. Matthew

3 From verbal discussion, the labelling of American Museum exhibition specimens and the captions to Pls. CIV and CV in Cope and Matthew (1915).

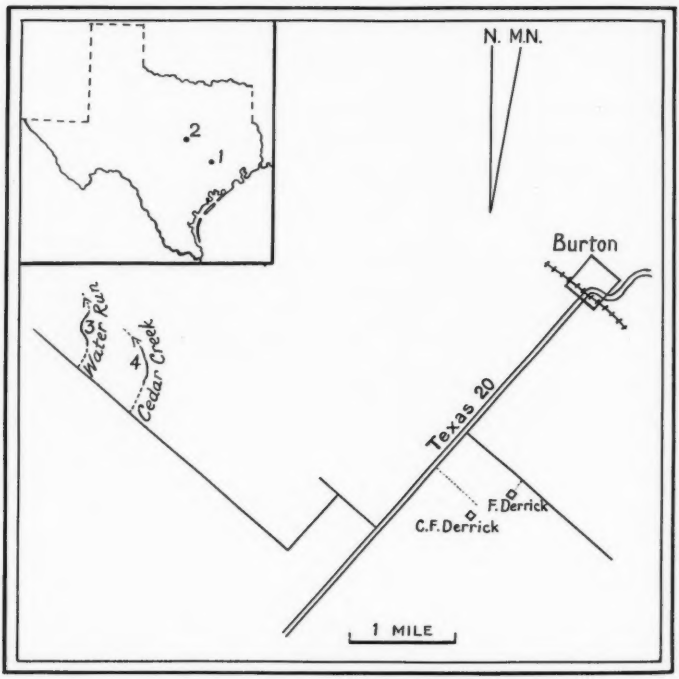


Fig. 1. Sketch map showing vertebrate localities in Washington County, Texas, Water Run (3) and Cedar Creek (4). Index map shows Washington County (1) and Coryell County (2).

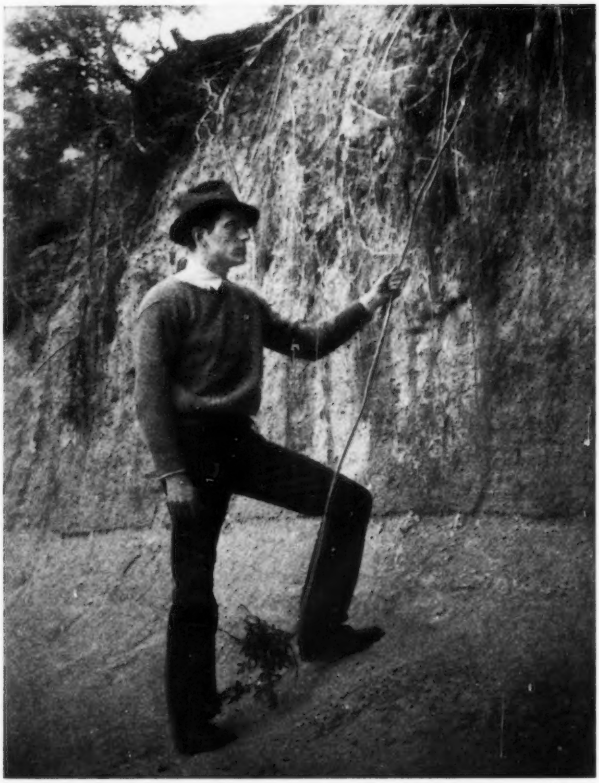


Fig. 2. Locality on Water Run where the *Caenopus* maxilla was found. View looking south-west.

has suggested (1931, p. 8) that "A better method would be to get it [*Caenopus*] on the list of 'nomina conservanda' with Leidy's classic species [*occidentalis*] as type and the fine skeleton[4] in the American Museum as the

4 This reference is obscure. It presumably refers to the composite mounted skeleton of *S. occidentalis*. Although much of the skeleton is Amer. Mus. No. 1132, the skull is Amer. Mus. No. 537. It is possible that Matthew had Amer. Mus. No. 538 in mind, which, although the skeleton of a single animal, is the type of *S. tridactylus*, a valid species, and hence not available as the neotype of *S. occidentalis*. In any case, this species is in no need of a neotype, as Leidy's figured skull, U. S. N. M. No. 114, treated as a cotype by Osborn (1898, pp. 150-153), as hautotype by Sinclair (1924) and neotype by Wood (1927, p. 63) is already available.

neotype of the species." Although any one is at full liberty to make such an appeal to the Commission, a favorable vote seems highly unlikely. It would be unusual, to say the least, to change an author's formally designated type species. *"Caenopus"* has had no such long-continued or exclusive use as to cause serious difficulty in the use of *Subhyracodon*. Thus casual inspection of Hay's two indices shows that *Aceratherium* was in almost universal use before 1904, and since then has probably been used as often as *Caenopus*, even if less judiciously. *Subhyracodon* has been used much less often than *Caenopus*, but is by no means an unknown or obscure name. Finally, article 32 of the International Rules of Zoological Nomenclature formally forbids suppression of a name because indicating "characters contradictory to those possessed by the animals in question." As far as this latter consideration goes, Brandt did not explain the derivative of *Subhyracodon*, so that it is not necessarily Sub + *Hyracodon* = ancestral — or near — *Hyracodon*, but can be interpreted as sub + Hyrax + odon = less specialized tooth than that of the hyrax, a name as applicable (or inapplicable) as *Hyracodon* itself. The similarity of *Prohyracodon* Koch to *Prothyracodon* Scott and Osborn is far more likely to cause confusion, but there has been no serious suggestion of requesting a special ruling in this latter case. Therefore, *Subhyracodon* is a valid name for a rhinoceros genus.

The course followed by Wood (1927 and 1929) was to regard the American Oligocene true rhinoceroses as separable into four groups, treated as genera, which are: (1) the primitive and relatively large *Trigonias*, continuing, with no great change except loss of front teeth, into (2) the large *Amphicaenopus;* (3) *Subhyracodon*, the best known line, of uncertain immediate ancestry, with the species *woodi, trigonodus, kewi, copei, occidentalis, gidleyi, metalophus* and *tridactylus*, merging, without a break, into the large diceratheres *(Diceratherium armatum*, etc.); and, (4) the small *Caenopus*, probably not derived from *Trigonias*, and, as first suggested by Peterson, quite likely ancestral to *Menoceras* (or *Diceratherium) cooki*. If anyone wishes to argue that *Caenopus, Subhyracodon* and *Amphicaenopus* rank only as "real" subgenera, there need be no serious argument, although publication of the criteria for definite discrimination between a "real" subgenus and a "real" genus would doubtless be welcomed by many perplexed workers. However, if *Amphicaenopus* is to be regarded as a subgenus, it should be a subgenus of *Trigonias*, to which its resemblance and relationships appear markedly closer than to either *Subhyracodon* or *Caenopus*, to which it is frequently referred. If the two latter are only subgenerically distinct, as may well be the case, *Caenopus* would be a subgenus of *Subhyracodon*, and not the reverse. However, there is no clear evidence as to just how close the relationship is between *Caenopus* and *Subhyracodon*, so that, for the present, it seems more convenient to leave them separate.

Gregory and Cook (1928) founded the species *?Caenopus premitis*, from the Chadron of Weld County, Colorado. Wood (1931) saw no more probable generic allocation. On the basis of "the admirable description of the dental and skull characters of specimen No. 1025 (E), C.M.N.H., from

Weld County, Colorado, by Gregory and Cook, plus Wood's sound logic that it is a distinctive form and is intermediate between *Trigonias* and *Caenopus," Figgins* (1934*a*) proposed the new genus *Procaenopus* for this species. Figgins (1934*b*, pp. 13-14, pl. III, fig. 1) offered as evidence for the validity of this genus as an "intermediate between *Trigonias* and *Caenopus (sensu strictu)"* (Wood, 1931, p. 426) resemblance to *"Caenopus"* from Torrington, which is, as a matter of fact, *Subhyracodon.* His only possibly significant evidence is the material, especially Colo. Mus. No. 1446, with only two upper incisors. Although he figures this premaxillary, no evidence of its specific identity with ?*C. premitis* has been published, other than Mr. Figgins' deter-

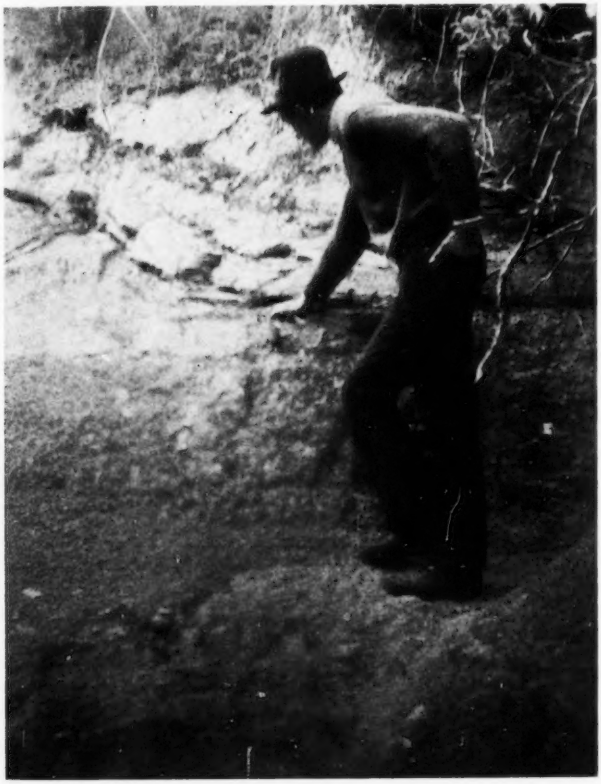


Fig. 3. Contact of Catahoula shales and Oakville sands on Cedar Creek, just downstream from the fossil locality in the base of the Oakville. Venard marking the contact between the two formations.

mination. As far as published evidence is concerned, this specimen might be referable to *Trigonias paucidens* or to *Subhyracodon trigonodus* or *copei*, or even to *Caenopus* (Wood, 1929, p. 71), all of which may have two upper incisors and the canine present together. The deep notch shown on the dorsal rim of the premaxilla, above I^1, is a rather common character in *Subhyracodon*, which genus is known from the Chadron.

Having determined what genera of American Oligocene true rhinoceroses are valid, the next problem is the disposition of *Caenopus persistens* Osborn (1904, pp. 318-319) from the Middle Miocene Pawnee Creek Beds of Logan County, Colorado. Wood (1927, p. 72) suggested that this form was a female dicerathere. It is also entirely possible that it belongs to the little-known assemblage of forms, of uncertain taxonomy, which intervene between the American Oligocene rhinoceroses and *Aphelops*. For the present, it may still be called ??*Diceratherium persistens* (Osborn).

Caenopus, s.s., is actually a rather rare genus. The known distribution (omitting doubtfully referred specimens, including the fore-leg referred to *A. mite* by Scott (1896), which while probably *Caenopus*, might belong to a small *Subhyracodon)* may be tabulated as follows:

Species	Formation	Region	Age	Specimen
C. dakotensis	Upper Brule	South Dakota	Upper Oligocene	Type, A. M. No. 1110
C. dakotensis	White River Group (not Oreodon zone)	Bad Lands	Upper Oligocene?	Berlin Museum
C. dakotensis	Upper Brule	South Dakota	Upper Oligocene	Field Mus. No. P. 12228
C. mitis	Chadron	Colorado	Lower Oligocene	Type and Paratype, A. M. No. 6325
C. mitis	Thompson[5] Creek	Montana	Lower Oligocene	C. A. Kinsey collection, Belgrade, Montana
C. mitis and "*pumilus*"	Cypress Hills	Saskatchewan	Lower Oligocene	Can. Geol. Surv.
?*C. premitis*	Chadron	Colorado	Lower Oligocene	Type, Colo. Mus. No. 1025 (E)
C. cf. ? premitis	Catahoula	Texas	Oligocene, level uncertain	U.S.N.M. No. 6573
C. yoderensis	Yoder	Wyoming	Basal Oligocene	M.C.Z. No. 2097

5 As this specimen, in the private collection of Mr. C. A. Kinsey, the zealous amateur naturalist of Belgrade, Montana, is not recorded, it is convenient to append the measurements here.

	$M\ \frac{}{1-3}$	M_2	M_3
Length	86 + mm.	28.3	30.9
Width	— —	19.6	17.3

In addition to the size, the absence of external and internal cingula is characteristic of *Caenopus*, s. s.

It is remarkable that, although *Caenopus* occurs in both the Lower and Upper Oligocene, it has not yet been recorded from the Middle Oligocene, in spite of the much more numerous fossils from that level. The Catahoula ocurrence cannot be assigned, on present information, to any special level in the Oligocene.

The Catahoula specimen consists of a left maxillary with all four premolars, of which the first and last are damaged (Figs. 4a and b). The rem-

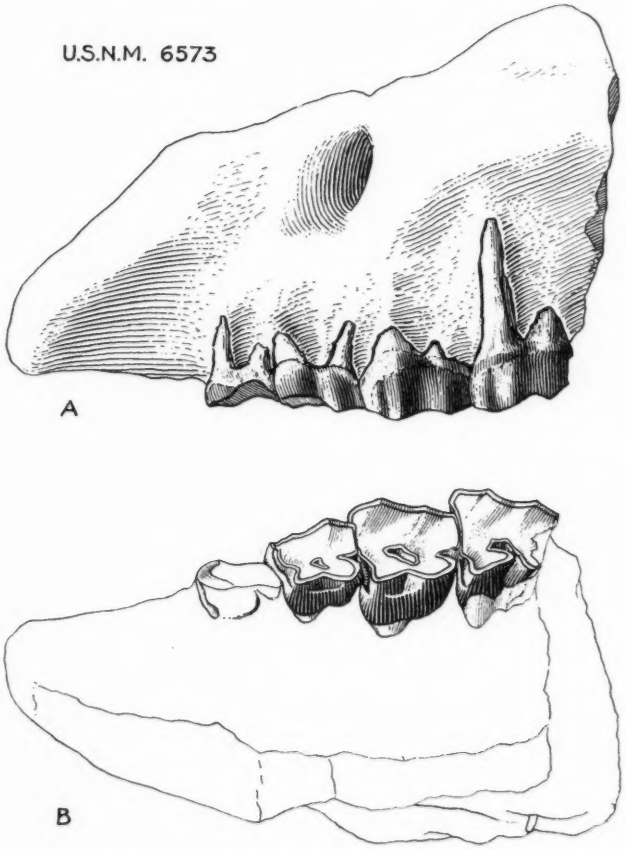


Fig. 4. (a). Lateral view of *Caenopus* maxilla, U. S. N. M. No. 6573, x 2/3. (b). Diagonal crown view of *Caenopus* maxilla, U. S. N. M. No. 6573, x 2/3.

nants of matrix consist of a nearly pure kaolin. The infraorbital canal opens above the posterior edge of P^2. The protocones of P^{2-4} are barely defined from the protoconules, anteriorly, by slight grooves. P^1 is large, retaining the primitive condition, but it is otherwise so worn as to be characterless. P^2 is well worn, with the medifossette already isolated and a strong internal cingulum across the median valley but entirely absent on the protocone and hypocone. The character of the tooth hints that the hypocone may have been more closely connected to the protocone than to the metaconule. The postfossette is divided into two parts by a ridge which is perhaps to be interpreted as the pseudocrista of Borissiak, 1914 (= metacrista, so named, independently, by Gregory and Cook, 1928, and by Teriaev, 1929, pp. 485-486). There is no external cingulum, and the anterior and posterior cingula are only moderately developed. Although P^3 is less worn than P^2, the medifossette is already isolated, so that the transverse lophs seems fully developed, but united by an incipient mure. There is a trace of an external cingulum; a moderate anterior cingulum and an internal one across the valley only are present, while the posterior cingulum appears only as the rear wall of the postfossette. The rear edge of P^4 is broken; the medifossette is not yet entirely isolated, the anterior face of the metaconule appears to be slightly crinkled, there is a trace of an external cingulum, a moderate anterior cingulum and none on the internal face of the protocone.

The fact that P^4 is as advanced as P^2, if not more so, the weak internal cingula and the small size, all indicate reference to *Caenopus, s.s.*, rather than to *Subhyracodon*. The specimen seems out of the probable size range of *C. dakotensis*. P^1 is much larger than in *C. mitis*, but the discrepancy diminishes toward the rear teeth. The most noticeable difference from ?*C. premitis* is the much weaker internal cingulum. Although it may be suspected that this specimen is of Upper Oligocene age and that it may quite possibly prove to be a distinct species, it seems best to call it *Caenopus* cf. ?*premitis* Gregory and Cook, until better evidence becomes available.

Comparative Measurements in Millimeters:

	?*Caenopus premitis*, type, after Gregory and Cook	*Caenopus* cf. *premitis*, U.S. N.M. No. 6573	*Caenopus mitis*, paratype, A. M. No. 6325		*Caenopus dakotensis* Berlin Mus.	
		Left	Right	Left	Right	Left
P^{1-4}	80.0	e82.0	69.3			
P^{2-4}	e64.0	e63.0	57.0		52.8	
P^1, AP	16.0	e18.7	12.5			
P^1, Tr.	15.0	e16.8	e11.5			
P^2, AP	17.0	19.4	17.2		15.4	
P^2, Tr.	26.0	m28.0	m25.0		19.7	
P^3, AP	20.0	22.0	19.3		18.6	18.3
P^3, Tr.	31.0	33.4	e28.0		26.1	26.0
P^4, AP	23.0	e20.5	20.6	21.7	19.2	19.2
P^4, Tr.	35.0	35.0	32.7	33.5	27.4	27.9

e = estimated
m = across metaloph

About a quarter of a mile east of the locality where the *Caenopus* was found, Mr. C. F. Derrick pointed out another locality, on Cedar Creek (Fig. 1). Here shales, apparently the same as the ones ocurring on Water Run, were overlain by about six feet of cross-bedded sands (Fig. 3), exposed for a distance of perhaps a hundred feet along Cedar Creek. At the contact between the sands and the shale, in most localities, was a deposit of black, asphaltic material, about a millimeter thick. The surface of the shales on which the sands rest is irregular, being a very obvious erosional surface. The sands seem to be stream-channel, probably estuarine. In these sands were found representatives of a considerable number of land mammals, mingled with freshwater and marine vertebrates. With practically no exception, the teeth were not water-rolled. Pieces of two teeth and one large limb bone fragment, of about the size to belong to a titanothere, elephant or such a large rhinoceros as *Metamynodon*, were so worn as to be unidentifiable, and may either have been transported for longer distances than the other specimens, or represent reworked fossils. In this small area, the following fauna was found in the course of an hour.

Land Forms

Horse: Amer. Mus. No. 30082, *Archaeohippus blackbergi* (Hay), new combination, right upper tooth, cf. M^3 (Pl. I, Fig. 1). *A. blackbergi* was described from the Garvin Farm, 2¼ miles north of Navasota, Texas. The resemblance is also close to *A. nanus* Simpson (1932, pp. 28-34), from the Hawthorn of Florida, which may be a synonym of *A. blackbergi*. This form is not greatly advanced over *Mesohippus stenolophus* Lambe (1905) from the Cypress Hills, and still less over *Miohippus equinanus* Osborn (1918) or *Parahippus pristinus* Osborn (1918), both from the Lower Rosebud. Half of a worn lower molar, Amer. Mus. No. 30083, suggests *Archaeohippus* (Pl. I, Fig. 2). A P_1 left, Amer. Mus. No. 30083, appears referable to this or some generally similar form (Pl. I, Fig. 3). There is also a fragment of a waterworn upper tooth (Amer. Mus. No. 30091), suggesting a somewhat larger horse (Pl. I, Fig. 4).

Deer: Amer. Mus. No. 30084, *Blastomeryx texanus* (Hay), new combination, worn but complete left M^2, and unworn left M^3 (Pl. I, Figs. 5-6). *B. texanus* was originally described from the Garvin Farm. *B. pristinus* Cook (1934) from the Lower Harrison may well be a synonym. Amer. Mus. No. 30085, *Blasteromeryx* cf. *primus* Matthew (1908, pp. 536-543), broken left upper molar, and a half left upper molar, a worn lower molar, an astragalus and a proximal phalanx, possibly referable to the same form (Pl. 1, Figs. 7-11). This species is known from the Upper Rosebud. The material also resembles *B. medius* Matthew (1924) from the Sheep Creek.

Peccary: Amer. Mus. No. 30086, talonid of left lower molar, probably a new genus, intermediate between *Desmathyus* of the Harrison and *Prosthenops* of the Upper Miocene (Pl. 1, Fig. 12).

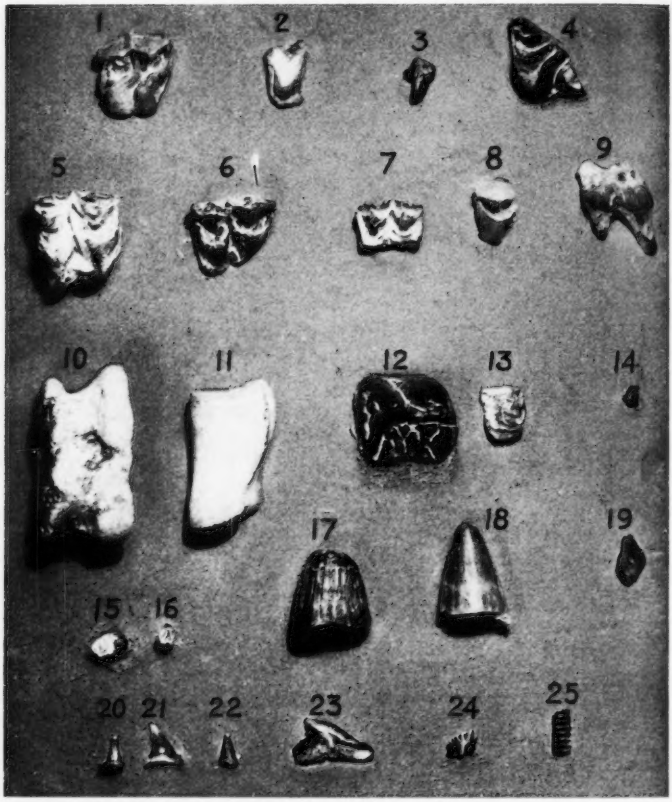


Plate 1. Teeth from the Oakville formation on Cedar Creek, x 1.

Figures: (1.) Amer. Mus. No. 30082, *Archaeohippus blackbergi* (Hay), M cf. 3/ right. (2.) Amer. Mus. No. 30083, cf. *Archaeohippus*, part of lower molar. (3.) Amer. Mus. No. 30083, cf. *Archaeohippus*, P/1 left. (4.) Amer. Mus. No. 30091, larger horse, upper tooth. (5.) Amer. Mus. No. 30084, *Blastomeryx texanus* (Hay), left M 2/. (6.) Amer. Mus. No. 30084, *B. texanus*, left M3/. (7.) *B.* cf. *primus*, Amer. Mus. No. 30085, part of left upper molar. (8.) *B.* cf. *primus*, Amer. Mus. No. 30085, part of left upper molar. (9.) *B.* cf. *primus*, Amer. Mus. No. 30085, lower molar. (10.) *B.* cf. *primus*, Amer. Mus. No. 30085, astragalus. (11.) *B.* cf. *primus*. Amer. Mus. No. 30085, proximal phalanx. (12.) Peccary, gen. indet., Amer. Mus. No. 30086, talonid of left lower molar. (13.) Dog, aff. *Tephrocyon*, Amer. Mus. No. 30087, right upper molar. (14.) ?*Palaeolagus* sp., Amer. Mus. No. 30089, M/1 right. (15.) *Palaeocastor* cf. *simplicidens*, Amer. Mus. No. 30088, P/4 left. (16.) *Palaeocastor* cf. *barbouri*, Amer. Mus. No. 30090, M ? 1/ right. (17-18.) *Alligator* ?? sp.,

Dog: Amer. Mus. No. 30087, right molar, which, acording to Mr. Childs Frick (letter dated Feb. 24, 1936) "suggests in a general way an upper first molar of some Lower Miocene precursor of *Tephrocyon*" (Pl. 1, Fig. 13).

Rabbit: Amer. Mus. No. 30089, *?Palaeolagus* sp. M_1 right (Pl. 1, Fig. 14). This is rather a primitive form, looking more like an Oligocene than a Miocene type, though the Lower Miocene rabbits are not well known. It seems nearer to *Palaeolagus* than to *Archaeolagus*.

Beaver: Amer. Mus. No. 30088, *Palaeocastor* cf. *simplicidens* (Matthew), P_4 left, cf. Stirton (1935), fig. 27. (Pl. 1, Fig. 15). *Palaeocastor* is known only from the Lower Miocene. It might occur in the Upper Oligocene, since we know very little of the Oligocene beavers, but could hardly occur much later than Harrison. Amer. Mus. No. 30090, *Palaeocastor* cf. *barbouri* (Peterson), ? M^1 right (Pl. 1, Fig. 16), cf. Stirton (1935, Fig. 39).

Rodent: incisor of a smaller form, size of a squirrel.

Freshwater Forms

Crocodilian: Amer. Mus. No. 1660, *Alligator* ??, two teeth (Pl. 1, Figs. 17-18).

Gar Pike: Amer. Mus. No. 30091, *Lepisosteus*, one scale (Pl. 1, Fig. 19).

These two forms are of no stratigraphic value, but are of definite ecological significance.

Marine Forms

Sharks: Amer. Mus. No. 30091, *Lamna* cf. *cuspidata* Agassiz, three small teeth (Pl. 1, Figs. 20-22), cf. Fowler, 1911, pp. 43-48, Figs. 12-15.

Amer. Mus. No. 30091, *Galeocerdo* cf. *aduncus* Agassiz, or *latidens* Agassiz, one tooth (Pl. 1, Fig. 23), cf. Fowler, 1911, pp. 67-71, Figs. 30-33.

Amer. Mus. No. 30091, cf. *Heptranchias primigenius* ? (Agassiz), one tooth (Pl. 1, Fig. 24), cf. Fowler, 1911, Figs. 1-7 and Agassiz, 1843, Pl. 27, Figs. 2, 6, and 16-17.

Ray: Amer. Mus. No. 30091, *Rhinoptera* cf. *dubia* Leidy, dental plate (Pl. 1, Fig. 25), cf. Fowler, 1911, pp. 102-105, Figs. 54-57.

These selachians are not very satisfactory horizon markers. All are fairly

---

Amer. Mus. No. 1660. (19.) *Lepisosteus* sp., Amer. Mus. No. 30091, a scale. (20-22.) *Lamna* cf. *cuspidata*, Amer. Mus. No. 30091, three small teeth. (23.) *Galeocerdo* cf. *aduncus* or cf. *latidens*, Amer. Mus. No. 30091, tooth. (24.) *Heptranchias primigenius* ?, Amer. Mus. No. 30091, tooth. (25.) *Rhinoptera* cf. *dubia*, Amer. Mus. No. 30091, dental plate.

frequent in Miocene formations of the Atlantic Coast, but they or very similar forms have a much wider time range.

This collection has a distinctly Lower Miocene aspect, most of the land forms being close to, if not identical with, forms from the Harrison of Nebraska. They also show considerable resemblance to part of Hay's Navasota material, from a nearby locality, the late aspect of which seems to indicate a mixture with later Miocene material. A similar appearance would result if the present fauna had been lumped with Leidy's later Miocene material from Washington County. There is some resemblance to the Florida Hawthorn (Simpson, 1932, pp. 13-16).

Besides the Catahoula *Caenopus* and the Miocene records cited above, there appear to be three records of Texas vertebrates of Oligocene or near-Oligocene age. Shumard (1863) mentions a Titanothere from Washington County, Texas. There is no mention of such an ocurrence in any of Leidy's discussions of Shumard's material (including Leidy 1860 and 1865) nor in his general monograph (1869), which indicates that Leidy considered either Shumard's record or his determination to be erroneous.

The second questionable Oligocene record is due to Schloenbach (1868), Roessler (1876) and Abel (1926).

Abel (1926) discusses and figures a skull of *Hyracodon "nebrascensis"* with badly worn teeth. This bears the "original" label:

"Skull of *Rhinoceros Nebrascensis* (Leidy) Loc: Coryell County, Texas A. R. Roessler collected 1863"

Abel states that this is the original of Leidy's figured specimen (1853, Pl. 15, Figs. 1-2) from the "Big Bad Lands," and that the label as to collector and locality is, therefore, wrong. There have been unpublished intimations that this is not Leidy's specimen, belonging to the Smithsonian Institution (Leidy, 1853, p. 14), collected by Dr. D. D. Owen. However, comparison of the specimen with Leidy's figures, which are of his usual high standard of accuracy, leaves no possible doubt that they are the same, even the breaks being identical. This specimen was part of a shipment of allegedly Texas fossils sent to the k. k. geologische Reichsanstalt of Vienna (now the geologische Bundesanstalt) by A. R. Roessler in 1868 (Schloenbach, 1868). The list of fossils is suspicious, on its face, as, in addition to what seems to be a typical collection of Big Badlands vertebrates *("Rhinoceros Nebrascensis, Oreodon major* and *gracilis, Anchitherium, Titanotherium* and *Testudo Nebrascensis")*, there is an obvious group of Mazon Creek, Illinois, plant concretions *("Pecopteris unita, villosa, Neuropteris hirsuta,"* "in Geoden"). Professor Abel arranged for the presentation of the *Hyracodon* to the American Museum, where it is now Amer. Mus. No. 22617.

What, at first glance, appears to be a third, independent, record, unpublished except for a glancing reference (Scott and Jepsen, 1936, p. 1[6]), is

6 This guarded reference was based on personal communications from the present authors, preceding the discovery of A. R. Roessler's activities.

provided by two oreodons in the paleontological collections of Columbia University. The label with one of these, a skull of *O. gracilis,* reads:

"Locality Cowhouse Creek *(reodon gracilis)* (Leidy) A. P. Roep"

The first two lines appear to be in Leidy's handwriting. "(Leidy)" and "A. P. Roep" are in two other hands. Closer inspection of "A. P. Roep," otherwise unknown, indicates that the label was torn twice across, through the "P" and through the end; that the "P" is a mutilated "R"; and that the "p" of "Roep" is an old-fashioned "ss," with the end of the label now missing, so that the name is, actually, "A. R. Roess. . . ." Comparison with Leidy's accurate figures once more shows that this is also from the Owen Big Badlands collection (Leidy, 1853, Pl. 5, Figs. 3-4, Pl. 6, Fig. 6), without possibility of error. The mandible, however, is now missing. The second Columbia specimen, a snout of *O. culbertsoni,* is labeled:

"*Oreodon gracilis,* Cowhouse Creek, Coryell Co., Texas."

There is also an old label, but distinctly more recent than the other. It seems rather likely that this is a misplaced label, originally associated with the other specimen. This snout was not figured by Leidy. These two oreodonts and the *Hyracodon* have every appearance of being typical Big Badlands specimens.

Cowhouse Creek, Texas, both inside and outside Coryell County, flows entirely within the Cretaceous, with no known Oligocene patches in the drainage area. In 1935 we were sufficiently open-minded about the possibility that an Oligocene patch might overlie the Cretaceous, as with other White River outliers, so that the junior author scouted along Cowhouse Creek, but without discovering any trace of such a deposit. It should be observed that the supposed Leidy handwriting gives no locality except "Cowhouse Creek." No record of a creek of that name has been found for the Big Badlands, either in contemporary maps or in the recollection of "old-timers." However, such a name might once have existed; or, as a more likely alternative, it might have been a mere collector's name, of which the exact application was afterwards totally forgotten. ("Marsh's Fork," a draw on Grizzly Buttes, West, Bridger Basin, Wyoming, a Yale collector's term of which the significance later became obscure, is a case in point.)

In view of the time elapsed, not all the steps in the original confusion can be legally proved, but the main facts are clearly demonstrable, and even the minor details seem strongly probable. What happened was about as follows. Dr. B. F. Shumard, who had been on the Owen Survey, and had considerable other experience, was appointed State Geologist of Texas on August 28, 1858. Among the subordinates that he appointed were S. B. Buckley and A. R. Roessler. On November 5, 1860, extracts from a letter from Shumard, dated October 2, 1860, were read before the St. Louis Academy of Science, announcing the discovery in Texas of "the existence of an extensive Miocene Formation, equivalent to the Bone beds of the Mauvaises Terres of Nebraska" (Shumard, 1863). This was the Washington County material collected in July, 1860 (Buckley, 1874, p. 8). Leidy first announced the same material,

sent to him by Shumard, before the Philadelphia Academy on October 9, 1860 (Leidy, 1860, 1865 and 1869). As Shumard believed that he had a Big Badlands fauna, it is entirely reasonable to suppose that he borrowed typical Badlands material for comparison, from the collections of the Owen Survey with which he had been associated, although there is no direct proof that he did so.

Meanwhile, as a result of political considerations (for details, compare Buckley, 1874; Hill, 1887; Merrill, 1920 and 1924; and Roessler, 1875), Dr. B. F. Shumard was replaced by Dr. F. M. Moore in November, 1860; then, in spite of spying on and talebearing about him by Buckley early in 1861 (Buckley, 1874, p. 9), the legislature reinstated Dr. Shumard on April 8, 1861, with instructions to wind up the survey by July 1, 1861. On the outbreak of the Civil War, Shumard, Moore, Buckley and Roessler went north, the Survey lapsed, and its quarters were turned into a percussion-cap factory.

It seems clear that Roessler looted the Texas Survey of specimens and maps, whether from loyalty to Shumard, dislike of Shumard's enemies, or simple thrift. There is no certainty whether Buckley shared in the loot (Roessler, 1875, p. 10). It is not so clear whether this took place at the outbreak of the Civil War, under the military occupation afterward, or at both times. "Early in January of 1866 I arrived in Austin, for the purpose of renewing the geological survey, found the specimens of the State collection in heaps, covered with dust, their labels displaced, and the most beautiful ones missing." (Buckley, 1874, p. 11.) "In March, 1874, Col. J. T. Brady, of Houston, informed Governor Coke and myself that, when he was in Washington, in December 1867, he saw in the possession of Roesler [sic] a large number of maps of Texas counties, also drawings of scenes in Texas, which were made when Roesler was employed as a draftsman for the State geological survey. . . . The specimens were arranged in natural groups in an upper room at the capitol, in 1867, since which time they have been very much disarranged, and, what is more unfortunate, many of the best specimens have been taken away; when, or by whom, I cannot tell. Col. Glenn told me that he thought several boxes of specimens had been taken away when the State was under military rule." (Buckley, 1874, p. 13.) As Roessler had become an at least fairly prominent employee of the General Land Office, at Washington, it might have been rather simple for him to arrange, either through a friend or through official channels, for the removal of his "personal" belongings from the Texas Capitol, during the military occupation. Any labels not already jumbled by the munitions workers could readily have been displaced by the soldiers doing the packing, who may have lacked exact scientific training.

On May 1, 1868, Roessler, who was an Austrian (Loew and Roessler, 1873, p. 454) wrote Director von Hauer of the k. k. geologische Reichsanstalt of Vienna a letter on Texas geology (Roessler, 1868), more or less plagiarized from Buckley, 1866. (Compare, especially, Roessler's fourth paragraph, page 189, with Buckley's second paragraph, page 33.) The interpretation of deliberate plagiarism, as opposed to independent, and probably un-

authorized, use of the same original field notes, seems fully established by Roessler's glossing over of the dates of publication in his reply to Buckley (Roessler, 1875, pp. 9-10). Cope's letter, which Roessler quotes as a complete exoneration, is carefully noncommittal.

About October, 1868, Roessler, for reasons which are purely speculative, sent the Reichsanstalt the collection of fossils, certainly *not* collected in 1863, as stated on the *Hyracodon* label!) listed by Schloenbach (1868). It is difficult to see how he could have regarded this collection as his own. It is reasonable to suppose that he did not know that there was any non-Texan material, and that as *O. gracilis* was labelled "Cowhouse Creek," Roessler assumed that it and similarly preserved material were from Cowhouse Creek, Coryell County, Texas. He had doubtless heard, without complete comprehension, of the Washington County fossil mammals. Roessler's actual accomplishments as a geologist were sufficiently slight, and Texas was then so little known, that he might readily not have seen any reason to doubt this assumption. (Cf. Roessler's geologic map, Loew and Roessler, 1873, Pl. 23, showing, among other less serious errors, the Permo-Triassic east of the Llano Estacado as Upper Cretaceous, and the Llano itself as granite and metamorphics.)

The exact date when, and mode by which, the oreodons entered the Columbia University collections is entirely unknown. However, as Roessler was a resident of New York City on February 1, 1875, on friendly terms with Dr. Newberry of Columbia College (Roessler, 1875, pp. 3 and 11), the link may readily be imagined.

This incursion into the early history of the Texas Survey, necessary to settle the Cowhouse Creek question, has led to the following judgments of the personalities involved, differing from those of Hill and Merrill, the chief historians of the Texas Survey, chiefly regarding the character and ability of A. R. Roessler. Dr. B. F. Shumard was an energetic, able and adequately trained geologist and paleontologist, by contemporary standards. Dr. F. M. Moore, whatever his personal and political accomplishments, was not fully qualified, by his long newspaper editorship, for the position of state geologist. Considered as geologists, both "Dr." S. B. Buckley and "Prof." A. R. Roessler were little more than pretentious charlatans. By his own confession (1874, p. 9), Buckley was a spy and a tale-bearer, under the guise of friendship, and his botanical publications and controversial style show a lack of scrupulous fairness. Whether or not Buckley did so, as Roessler charges (Roessler, 1875, p. 10), Roessler made singularly free with specimens and maps to which his claim was limited, to say the least, and, despite his professed opinion of Buckley's geological ability, he plagiarized Buckley's work for publication abroad, in German. It might, however, be urged in Roessler's defense that he was preternaturally farsighted, as, whatever he did not remove was destroyed in the capitol fire of 1881 (Hill, 1887, pp. 36-37). It is certainly true that the conditions were unusual, and that there may have been legitimate conflicts of loyalty.

In conclusion therefore, with this demonstration of the entirely fictitious

character of the supposed continental Oligocene of Cowhouse Creek, Coryell County, the upper Catahoula and lower Oakville levels, described above, yield the earliest land mammals yet known from Texas, and should assist in intercorrelating the continental and marine sequences. The collection from the base of the Oakville extends the range of the Lower Miocene Harrison fauna six hundred miles to the south.

REFERENCES[7]

ABEL, O. 1926—Die Molarisierung der oberen Prämolaren von *Hyracodon nebrascensis* Leidy. Palaeont. Zeit. **8**(3):224-245. Pp. 241-242: skull, which Abel regards as Leidy's original type of *H. nebraskensis*, bearing label from Coryell County, Texas.—A. R. Roessler collected 1863.

AGASSIZ, L. 1843—Recherches sur les Poissons Fossiles. III, atlas. Neuchatel, 4°.

APLIN, P. L. 1925—The Stratton Ridge salt dome, Brazoria County, Texas. Bull. Amer. Ass. Petr. Geol. **9**:1-34. P. 22, Stock on vertebrates; *Merychippus* tooth.

BORISSIAK, A. 1914—Sur la dentition d'*Elasmotherium caucasicum* n. sp. Bull. Acad. Imp. Sci. St.-Pétersburg, (6), **8**(9):555-586, fig. 1 and pls. I-II.

BRANDT, J. F. 1878—Tentamen Synopseos Rhinocerotidum viventium et fossilium. Mém. Acad. Imp. Sci. St.-Pétersbourg, (7), **26**(5):1-66, 1 pl.

BUCKLEY, S. B. 1866—A Preliminary Report of the Geological and Agricultural Survey of Texas. Star Gazette, Austin, 8vo., pp. 1-81 + 6. See especially pp. 5 and 33.

———1874—First Annual Report of the Geological and Agricultural Survey of Texas. A. C. Gray, Houston, 8vo., pp. 1-142. See especially pp. 6-14 and 64.

COOK, H. J. 1934—New Artiodactyls from the Oligocene and Lower Miocene of Nebraska. Amer. Midl. Nat. **15**(2):148-165, pls. III-IV.

COPE, E. D. 1879—A new genus of Perissodactyla. Amer. Nat. **13**:270-271.

———1880—The genealogy of American rhinoceroses. Amer. Nat. **14**:610-611.

———1891—On vertebrata from the Tertiary and Cretaceous rocks of the North West Territory. Contr. to Canadian Pal., Geol. Surv. Can., III. (I. The Species from the Oligocene or Lower Miocene beds of the Cypress Hills.) pp. 1-25, pls. I-XIV. See pp. 19-20 and pl. IV, figs. 2-4.

COPE, E. D. AND W. D. MATTHEW. 1915—Hitherto unpublished plates of Tertiary mammalia and Permian vertebrata. Amer. Mus. Nat. Hist., Monog. Ser., No. 2., pls. I-CLIV.

DEUSSEN, A. 1924—Geology of the coastal plain of Texas west of Brazos River. U.S. Geol. Surv., P. P. **126**:1-139, pls. I-XXXVI. Catahoula and Oakville formations, pp. 95-99; *Caenopus* maxilla, Gidley's report, p. 98 and pl. XXVIII, figs. 1, 1a and 1b.

[7] The following paper has just become available to the authors: Renick, B. C. 1936. The Jackson Group and the Catahoula and Oakville Formations in a part of the Texas Gulf Coastal Plain. Univ. Texas Bull. 3619, pp. 1-104, Pls. I-X. See especially, pp. 69-70, 72-73, 81-84 and Pls. I-III. After a visit to the Derrick Farm, Renick agrees emphatically that the Water Run *Caenopus* locality is within the Catahoula, and places it, stratigraphically, about the middle of the formation (Pl. III, section 6). Our Cedar Creek locality is presumably in his "Basal Oakville Sandstone," his map (Pl. II) to the contrary. We see no reason for modifying our age determinations.

DUMBLE, E. T. 1903—Geology of Southwestern Texas. Trans. Amer. Inst. Mining Eng. **33**:913-987. P. 957, Leidy's fossils with revised determinations.

———1915—Problem of Texas Tertiary sands. Bull. Geol. Soc. Amer. **26**:447-476. Pp. 470-472 vertebrate localities; Hay's citation (1924) of Matthew (1920) refers to Matthew's determination given here on page 471.

———1918—The Geology of East Texas. Univ. Texas Bull. **1869**, 388 pp., map. Cites Matthew on vertebrates, pp. 230-233, 236-238 and 242.

FIGGINS, J. D. 1934a—The Generic Status of *?Caenopus premitis*. Proc. Colo. Mus. Nat. Hist. **13**(1):1.

———1934b—New Material for the Study of Individual Variation, from the Lower Oligocene of Colorado. Proc. Colorado Mus. Nat. Hist. **13**(3):7-14, pls. I-III.

FOWLER, H. W. 1911—A description of the fossil fish remains of the Cretaceous, Eocene and Miocene Formations of New Jersey. Geol. Surv. N. J. Bull. **4**:5-192.

GREGORY, W. K. AND H. J. COOK. 1928—New Material for the Study of Evolution: A Series of Primitive Rhinoceros Skulls *(Trigonias)* from the Lower Oligocene of Colorado. Proc. Colorado Mus. Nat. Hist. **8**(1):3-32, pls. I-VI.

HAY, O. P. 1924—Description of some Fossil Vertebrates from the Upper Miocene of Texas. Proc. Biol. Soc. Washington **37**:1-19, pls. I-VI.

HILL, R. T. 1887—The Present Condition of Knowledge of the Geology of Texas. U. S. Geol. Surv. Bull. **45**:5-95. First and second geological surveys, pp. 29-42.

LEIDY, J. 1853—The Ancient Fauna of Nebraska. Smithsonian Contr. Knowledge **6**:1-126, pls. I-XXIV. The "Coryell County, Texas" *Hyracodon nebraskensis*, pp. 86-87, pl. XV, figs. 1-2. The "Coryell County, Texas" *Oreodon gracilis*, p. 54, pls. V, figs. 3-4 and VI, figs. 6-7.

———1860—[Three fossil teeth from Washington Co., Texas.] Proc. Acad. Nat. Sci., Philadelphia **12**:416.

———1865—[Fossil remains of Rhinoceros from Texas and California.] Proc. Acad. Nat. Sci., Philadelphia, **17**:176-177. *Rhinoceros meridianus* described from Washington County, Texas.

———1869—The extinct mammalian fauna of Dakota and Nebraska. Journ. Acad. Nat. Sci., Philadelphia, (2), **7**:1-472, pls. I-XXX. Pp. 229, 298, 312-313 and 402, pls. XVII, figs. 3-7, XVIII, figs. 51-53, XXI, fig. 13, and XXIII, fig. 10, deal with Shumard's material from Washington County, Texas.

LOEW, O. AND A. R. ROESSLER. 1873—Erforschung des Nordwesttheiles von Texas im Jahre 1872. Petermann's Mittheilungen **1873**:453-467, pl. XXIII. See especially pp. 454, 466-467 and pl. XXIII.

MATTHEW, W. D. 1908—Osteology of *Blastomeryx* and Phylogeny of the American Cervidae. Bull. Amer. Mus. Nat. Hist. **24**(27):535-562.

———1931—Critical observations cn the phylogeny of the Rhinoceroses. Univ. California Publ. Geol. **20**(1):1-9.

MERRILL, G. P. 1920—Contributions to a History of American State Geological and Natural History Surveys. U. S. Nat. Mus. Bull. **109**:1-549. First and second Texas surveys, pp. 471-480.

———1924—The First One Hundred Years of American Geology. Yale Univ. Press, 8vo., pp. 1-773. Texas Survey, pp. 371-372, 401-402, 686-687.

OSBORN, H. F. 1898—The Extinct Rhinoceroses. Mem. Amer. Mus. Nat. Hist. **1**(3): 75-164, pls. XIIa-XX.

———1904—New Miocene Rhinoceroses with Revision of Known Species. Bull. Amer. Mus. Nat. Hist. **20**(27):307-326.

PLUMMER, F. B. 1932—Cenozoic Systems in Texas. Part 3 of SELLARDS, E. H., W. S. ADKINS and F. B. PLUMMER, The Geology of Texas. I. Stratigraphy. Univ. Texas Bull. **3232**:519-818. See pp. 710-749.

ROESSLER, A. R. 1868—Geologische Untersuchungen in Texas. Verhandl. k. k. geol. Reichsanst. Wien **1868**(9):188-190.

———1875—Reply to the charges made by S. B. Buckley, State Geologist of Texas in his official report of 1874 against Dr. B. F. Shumard and A. R. Roessler. New York, 8vo., pp. 3-12, privately printed.

———1876—Beschaffenheit und geologische Verhältnisse des Sauersees in Hardin County, Texas. Verhandl. k. k. geol. Reichanst. Wien **1876**(10):227-229. P. 229, Texas equivalents of Mauvaises Terres.

SCHLOENBACH, U. 1868—A. R. Rössler's Sendung von Versteinerungen aus Texas. Verhandl. k. k. geol. Reichsanst. Wien **1868**(14):356.

SCOTT, W. B. 1896—Die Osteologie von Hyracodon Leidy. Festschrift zum 70. Geburstage von Carl Gegenbaur **2**:353-384, pls. I-III.

SCOTT, W. B. AND G. L. JEPSEN. 1936—The Mammalian Fauna of the White River Oligocene. Part I. Insectivora and Carnivora. Trans. Amer. Phil. Soc., n.s., **28**(1):1-153, pls. I-XXII.

SHUMARD, B. F. 1863—[Discovery in Texas of dicotyledonous leaves in Cretaceous strata and the existence of an extensive Miocene formation, equivalent to the bone beds of the Mauvaises Terres of Nebraska.] Trans. Acad. Sci. St. Louis [for Nov. 5, 1860] **2**:140-141.

SIMPSON, G. G. 1932—Miocene Land Mammals from Florida. Florida State Geol. Surv. Bull. **10**:7-41.

SINCLAIR, W. J. 1924—The Faunas of the Concretionary Zones of the Oreodon Beds, White River Oligocene. Proc. Amer. Phil. Soc. **63**(1):120-121.

STIRTON, R. A. 1935—A review of the Tertiary Beavers. Univ. California Publ. Geol. **23**(13):391-458.

TERIAEV, W. A. 1929—[On the dental structure and synonymy of *Elasmotherium* Fisch. and *Enigmatherium* M. Pavlow. (Trans.)] Bull. Soc. Nat. Moscou, Sect. Geol., **37**:465-496, figs. 1-12. (Russian only.)

WEEKS, A. W. 1933—Lissie, Reynosa, and Upland Terrace Deposits of Coastal Plain of Texas between Brazos River and Rio Grande. Bull. Amer. Ass. Petr. Geol. **17**(5):453-487. See pp. 456, 459-460.

WOOD, H. E. 1927—Some Early Tertiary Rhinoceroses and Hyracodonts. Bull. Amer. Paleont. **13**(50):5-105.

———1929—American Oligocene Phinoceroses—a Postscript. Journ. Mam. **10**(1): 63-75.

———1931—Lower Oligocene Rhinoceroses of the Genus *Trigonias*. Journ. Mam. **12**(4):414-427.

WOOD, H. E. AND A. E. WOOD. 1936—Middle Tertiary Vertebrates from the Texas Coastal Plain. Proc. Geol. Soc. Amer. **1935**:396.

UNIVERSITY OF NEWARK
AND
U. S. ARMY ENGINEERS
NEWARK, N. J.

Tracks from the Pliocene of West Texas

C. Stuart Johnston

The fossil tracks described in this paper are unusually perfect, and well-preserved. However their chief importance lies in the fact that they were found closely associated with the fossil remains of the group of vertebrates to which they belong. The tracks were discovered in the summer of 1935, and collected by the field party of the West Texas State Teachers College. The first of these tracks to be discovered, that of a cat, was pointed out by Professor R. A. Stirton and his assistants, of the University of California while visiting the location. The fossil beds in which they occur are located in Hemphill County, Texas, on the Coffee Ranch, about 9.3 miles north of the town of Miami.

The location mentioned above is one of the most important in West Texas, and has been worked by several institutions since its discovery a number of years ago. The fossils are abundant, and though fragile and poorly preserved are representative of a varied assemblage of the animal life of Middle Pliocene time. Since the tracks are found immediately above the bone bed it would be worthwhile to list the more important families that are represented. The following list is from Matthew and Stirton (1930).

Canidae: *Borophagus cyonoides*
Ursidae: *Hyaenarctos*, sp.
Felidae: *Machaerodus catocopis*
Mylagaulidae: *Mylagaulus* cf. *monodon*
Equidae: *Pliohippus interpolatus*
Hipparion lenticulare
Hipparion eurystyle
Rhinocerotidae: *Aphelops* cf. *mutilus*
Mastodontidae: *Rhyncotherium* ?
Tagassuidae: *Prosthennops* ? sp.
Camelidae: *Paracamelus*, sp.
Alticamelus ?, sp.
Procamelus ?, sp.
Antilocapridae: *Merycodontinae*,
Cervidae: *Dyseomeryx*? sp.

The formation bearing the tracks is of Middle Pliocene age, and the bed in which they occur consists of fine, volcanic ash. It is thinly bedded, and many of the bedding planes show very distinct ripple marks. The ash bed is about five feet in thickness, and rests conformably upon a four foot stratum of light gray clay. The clay in turn overlays the bone bearing formation which is made up principally of very fine grained, semiconsolidated sand of gray color. The tracks are thus located approximately eight feet above the fossil horizon, which is near the base of the gray sand. This is locality No. 20 of No. 1 bed according to Reed and Longnecker (1932). It may be seen from a study of the fauna of this horizon that the tracks obviously belong to some of the same genera if not indeed, to the same species of animals found fossil in this formation.

Most of the tracks are found on a single bedding plane which averages approximately eight inches above the base of the volcanic ash. A few others, however, have been found above this level. They are unusually clear and

well-preserved, thus making possible a high degree of accuracy in their measurements. As pointed out by Gidley (1903) most of the Tertiary formations of the Staked Plains are of fluvial origin, and this is certainly true of the beds with which we are here concerned. Furthermore, they were deposited in water of shallow depth, and must have been in a damp, slightly plastic condition at the time when the tracks were made. As there is no evidence of erosion or sun-cracking on this surface it would appear that the tracks were covered shortly after they were made by a protecting layer of water laid ash.

The families represented by these tracks are the *Canidae*, the *Felidae*, the *Mastodonidae*, the *Camelidae*, the *Equidae*, and also one group of birds which were probably crane-like in habit.

The tracks here referred to the Canidae seem to belong to *Borophagus cyonoides* Martin, as described by Matthew and Stirton (1930). In a subsequent paper Stirton and Vanderhoof (1933) founded a new genus to replace *Borophagus* to which much of the Hemphill material had been referred. The new genus is *Osteoborus*, and hence the form mentioned above becomes *Osteoborus cyonoides*. This is the typical member of the Canidae found at this locality, and the size of the tracks would seem to indicate an animal of about the proportions of *Osteoborus*.

As far as the tracks indicate, the Felidae are represented by two different types. The largest of these evidently belongs to the fairly well-known *Macharodus catacopis* Cope, as described by Burt (1931). The second group of cat tracks is much smaller, and fossils representing them are fragmentary in the locality. They indicate an animal somewhat smaller than a mountain lion.

The only undoubted Proboscidean tracks found here are tentatively referred to *Rhyncotherium*. The tracks are clear and definite, and there can be but little doubt that they belong to some member of the Mastodontidae. Fossil representatives of the group, however, are rare, and exceddingly fragmentary, and definite identifications are consequently difficult.

Only two tracks have been found which are thought to represent the family Camelidae. There is but little doubt that the tracks are those of some member of the artiodactyls. They are large enough to belong to *Alticamelus*, but that they are actually camel tracks is open to question.

The Equidae are abundant in the fauna, and a fine collection of material has been collected here and described by Stirton (1930). However, only one track has been found that can be placed in this group. While it is clear in outline and definite in its hoof-like shape, it would be desirable to find others like it before classifying it certainly as that of a horse.

Two bird tracks were found, both of which were on the same slab of rock, and no doubt belong to the same individual. These tracks are thought to be those of a wading bird, a type perhaps not differing greatly from the cranes. The author is not aware of fossil birds having been found in the locality.

Figs. 1 and 2 are the positive and negative tracks of *Osteoborus cyonoides* Martin. The track in the lower part of the figure is 8 cm. in width and 9 cm. in length. The track just above it is 7.7 cm. and 8 cm. in length. At the top of the figure is an impression which resembles that of a small horse. It has a width of 5.6 cm. and a length of 6.2 cm.

Fig. 3 is a slab containing a number of cat tracks of unidentified species. The track in the center is the discovery track. It is 8.5 cm. in width, and 7.7 cm. in length.

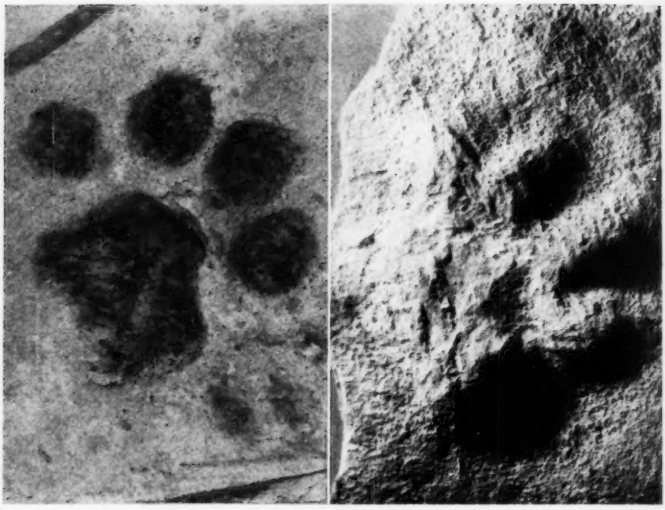


Fig. 1 is a large cat track, probably *Machaerodus catocopis* Cope. Width 13.2 cm., length 11 cm.

Fig. 2 is identified as belonging to some member of the artiodactyls. It is not as distinct as the others, and it will be necessary to find more specimens like it before identifications can be made with certainty. Width 17.7 cm., length 16.6 cm.

Fig. 3, a mastodon track, probably *Rhyncotherium*. Width 23.6 cm., length 21 cm.

Fig. 1. This slab contains a number of dog tracks, *Osteoborus cyonoides*, and a cat track in the lower left. Measurements are as follows: track in the lower right, width 6.4 cm., length 6.6 cm.; lower left, width 8.4 cm., length 8.5 cm.; upper right, width 8.5 cm., length 8.5 cm.; upper left, width 7 cm., length 7 cm.

Fig. 2. These are bird tracks, species unidentified. The track in the right of the figure, width 9.2 cm., length 8.2 cm.; track in the left of the figure, width 9.2 cm., length 7.9 cm.

REFERENCES

BURT, WILLIAM HENRY. 1931—Machaerodus catacopis, Cope, from the Pliocene of Texas. Bull. Univ. Cal. **20**(7).

GIDLEY, J. W. 1903—The Fresh-Water Tertiary of Northwestern Texas. Bull. Amer. Mus. Nat. Hist. **19**(26).

MATTHEW, W. D. 1932—A Review of the Rhinoceroses with a Description of Aphelops Material from the Pliocene of Texas. Bull. Univ. Cal. **20**(12).

———AND R. A. STIRTON. 1930—Osteology and Affinities of Borophagus. Bull. Univ. Cal. **19**(7).

———AND R. A. STIRTON. 1930—Equidae from the Pliocene of Texas. Bull Univ. Cal. **19**(17).

REED, LYMAN C. AND OSCAR M. LONGNECKER, JR. 1932—The Geology of Hemphill County, Texas. Bull. Univ. Texas. **3231**.

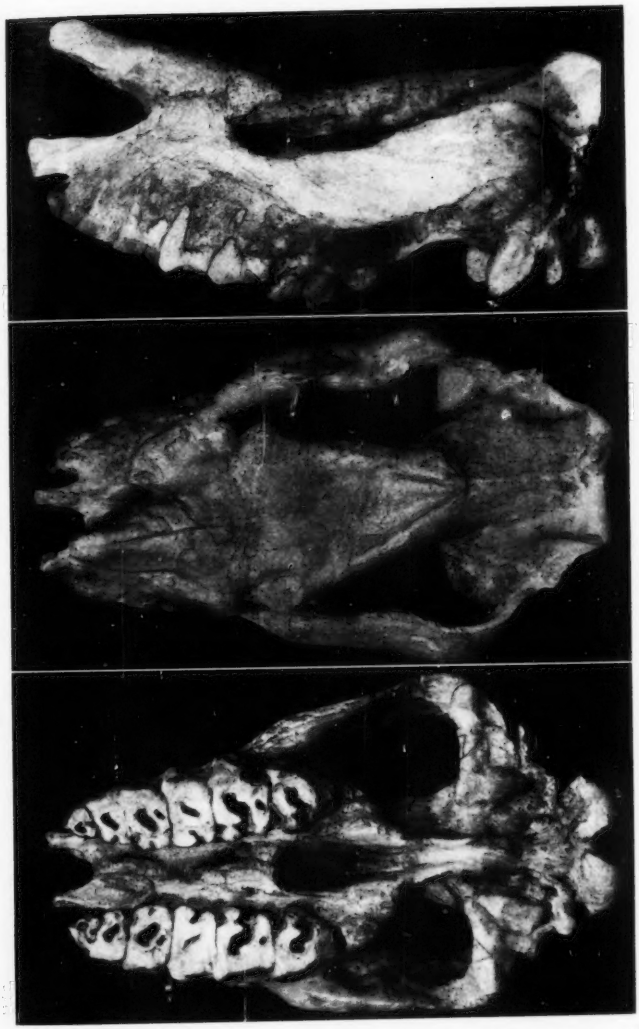
STIRTON, R. A. AND V. L. VANDERHOOF. 1933—Osteoborus, a new Genus of Dogs, and its Relations to Borophagus Cope. Bull. Univ. Cal. **23**(4).

WEST TEXAS STATE TEACHERS COLLEGE,
CANYON, TEXAS.

A Skull of Teleoceras fossiger Cope, from the Clarendon Beds of Donley County, Texas

C. Stuart Johnston

During the spring and summer of 1935 the West Texas State Teachers College, in cooperation with the Federal Relief Administration maintained a field party at Clarendon, Texas. The work was devoted entirely to the collection of vertebrate paleontological material of Lower Pliocene age. Most of the collecting was done in a quarry located on what is known as Spade Flats, on the Lewis Ranch, about twenty-four miles northeast of Clarendon. The project was under the supervision of Mr. Will Chamberlain, directed by the author. Much fine material was collected, all of which was placed in the Panhandle Plains Historical Society Museum at Canyon, Texas. Among other specimens collected was the almost perfect skull of *Teleoceras fossiger* Cope. This form is fairly well known from numerous skulls, and the description of a complete skeleton by Osborn (1898). However, there is considerable variation and it is considered worthwhile to add any data possible to our knowledge of its generic and specific characters.



Figs. 1, 2, and 3, lateral, dorsal, and palatal views of *Teleoceras fossiger* Cope. 1/6 natural size.

MEASUREMENTS:

Length of skull from occipital condyles to end of nasals.	541 mm.
Breadth of skull opposite M3	277
Greatest breadth across the zygomatic arches	323 mm.
Height of zygomatic arch	85
Breadth of frontals between the postorbital processes	174
Length of saggital crest from the intersection of the temporal impressions to the beginning of the lambdoidal crest	100
From anterior end of nasals to intersection of temporal impressions	363
Breadth of lambdoidal crest	80
Width of skull 10 mm. below enterior edge of orbits	185
Length of temporal impressions from their intersection to postorbital processes	190
Breadth of cranium opposite intersection of temporal impressions	94
Height of skull from ventral side of occipital condyles to dorsal edge of lambdoidal crest	207
Vertical diameter of orbit	49
Anterior edge of orbit to anterior edge of nasals	168
Length of palate	181
Breadth of palate opposite anterior edge of M2	71
Greatest breadth of postpalatal notch	44
Depth of postpalatal notch	132
Breadth of occipital condyles	139
Between occipital condyles at middle of foramen magnum	59
Length of dental series	264

DENTAL MEASUREMENTS:

	P1	P2	P3	M1	M2	M3	
Length	31	32	43	40	53	60	mm.
Breadth	31	46	59	62	70	78	mm.

As shown in the photographs there is some slight distortion in the skull, particularly on the right side. Otherwise it is practically in perfect condition, and such restoration as it has received is negligible, and has not influenced in any way the above measurements.

As pointed out by Matthew (1932) there is considerable variation in the craniometry of the Rhinocerotidae. It is the author's opinion that the limits of these variations can only be defined, and the specific and generic characters of a form determined through the careful study of as large a body of data as possible. Toward this end the above notes on *Teleoceras fossiger* Cope are submitted.

REFERENCES

MATTHEW, W. D. 1932—A Review of the Rhinoceroses with a Description of Aphelops Material from the Pliocene of Texas. Bull. Univ. Cal. **20**(12).

OSBORN, HENRY FAIRFIELD. 1898—A Complete Skeleton of *Teleoceras fossiger*. Notes upon the growth and Sexual Characters of this Species. Bull. Amer. Mus. Nat. Hist. **10**(4).

WEST TEXAS STATE TEACHERS COLLEGE,
CANYON, TEXAS.

Spores from the Pennington Coal, Rhea County, Tennessee

Willard Berry

The Pennington coal, which is exposed in the floor of Cranmore Cove, Rhea County, Tennessee, occurs as a thin vein, with a maximum thickness of 52 inches. This coal lies approximately 100 feet above the Bangor limestone of the Chester series and about 350 feet below the Gizzard formation of the lower Pottsville, and is considered as Lower Carboniferous (Mississippian) in age; though there is no definite break either above or below. The coal is locally mined but as far as I know there are no published analyses of it.

This coal can readily be macerated and the resulting material mounted in glycerine jelly for study. In this manner I have found 14 different species of spores. These spores can be separated into the following 6 groups on their general shape and structure. *Tuberculati-sporites* with 1 species, *Zonales-sporites* with 4 species, *Laevigato-sporites* with 3 species, *Denso-sporites* with 3 species, *Elongato-sporites* with 1 species, and *Sporonites* with 2 species. *Zonales-sporites* are the most common followed by species of *Denso-sporites* and then *Elongato-sporites*, with the other forms fairly rare. All the forms are new although similar types have been figured from other localities but not described. No attempt has been made to make a spore profile for the coal as suitable material is not available.

Systematic Description

Genus *Tuberculati-sporites* Ibrahim 1933

Tuberculati-sporites tuberculatus sp. nov.

Fig. 6

Oval, about one and three-quarter times as long as broad; wall very thin; surface tuberculate, tubercles however not visible over the edges of spore although they probably are present; small crack running in a short distance from each end. Color, yellowish brown. Length of the figured specimen 54μ, width 39μ.

This ovoid spore looks as if it was entirely broken around on the side away from the observer. I have not found any specimens which show a split on the visible side. Even though these specimens are rare, it seems to me that in chance arrangements both sides must appear, and yet in all observed cases no complete split was seen. This is the only tuberculate form found in the coal. Slide L2 (77x52.3).

Somewhat like *Sporonites abditus* Loose (1932, p. 451, fig. 53) but lacking the triradiate split.

Genus *Zonales-sporites* Bennie & Kidston 1886

Zonales-sporites Priddyi sp. nov.

Fig. 2

Spore triangular; wall very thin, often slightly convex between angles; surface clear, smooth; triradiate split, branches reaching about two-thirds of way from the center to the margin. Height of spore up to 35μ.

These spores often occur as dense closely packed masses with a few scattered about the main mass. They are somewhat like *Sporonites sphaerotriangulus Loose* (1932, p. 451, fig. 45) except much larger.

Slide L1 (91x49.4).

Zonales-sporites penningtonensis sp. nov.

Fig. 3

Spore round, with a thin wall; and a very narrow keel like wing; triradiate split, branches reaching to wing; surface smooth. Diameter 40-44μ.

This is a rather common form and all observed specimens were within a few microns of the same size.

Slide L1 (96x52.3), L1 (91.7x49.6).

Zonales-sporites peacocki sp. nov.

Fig. 5

Spore roundly triangular; wall thin; surface rought or slightly reticulate: triradiate split, branches not quite reaching to margin; central part surrounded by a clear wing; narrow at the angles, wider between. Diameter about 31μ.

This species is not rare in this coal. It is somewhat like *Z. Priddyi* but is winged and has a reticulate surface. It is somewhat like a form figured by Reinsch (vol. I, p. 3, pl. 2, fig. 18; p. 3, pl. 1, fig. 11) from "Devonian" coal from Central Russia.

Slide L1 (85.3x46.2).

Zonales-sporites irregularis sp. nov.

Fig. 9

Spore roundly triangular; wall thin; surface smooth except quadrant "a" where surface is granular; triradiate split, branches reaching nearly to the margin; on the margin of the granular surfaced quadrant "a" a narrower wing and directly across the spore a similar though shorter, narrower wing. Diameter 39μ.

This form is rare in this coal. However the few that I have found lead me to think it is a distinct species.

Slide L1 (94.6x50).

Genus *Laevigato-sporites* Ibrahim 1933

Laevigato-sporites pennovalis sp. nov.

Fig. 4

Spore oval; wall thicker at ends than at sides; surface sparingly covered with very small papillae, more or less evenly spaced, not visible at margins.. Length 46μ; breadth 31μ.

This species, which is rare, takes up stain like many grains from rocks of younger geological ages. It is quite like *Laevigato-sporites vulgaris* Ibrahim (1933, p. 39, fig. 16) but lacks the opening.

Slide L1 (87.6x46.8).

Laevigato-sporites cranmorensis sp. nov.

Fig. 1

Spore oval, almost as broad as long; slightly indented at one end; wall thin, clear; end away from identation has what appears to be a slit or crack extending in about three-fourths the length of the grain; this slit is in part at a very low angle to the surface. On the figured specimen another line is present, but is not present on all specimens. Length about 58μ; breadth 42μ.

This species is relatively rare here but is quite like some unpublished forms from the Washington Coal (Dunkard, Permian) of Eastern Ohio.

Slide L2 (78.5x50.3).

Laevigato-sporites rheaensis sp. nov.

Fig. 13

Spore elongate oval, lemon shaped; about three-fourths longer than broad; surface "a" translucent, yellowish brown separated by a definite boundary from "b" where the wall is dense and opaque with a smooth surface; the boundary line may represent the opening into the grain; it does not as far as observed represent a broken part of the surface. Length about 43μ; breadth 27μ.

This species is rare but quite distinctive.

Slide L1 (79.9x51.4).

Genus **Denso-sporites** gen. nov.

Characterized by a thick opaque wall, thickness about one-third the diameter of spore; central portion clear, no triradiate split. Genotype: *Denso-sporites covensis*.

Denso-sporites covensis sp. nov.

Fig. 11

Spore oval; wall very thick, about one-third of diameter, very dark and opaque, very smooth and even; central portion more or less clear and roughly trapezoidal in shape, margins very clearly marked, no apparent connection between inside and outside. Length about 58μ; width 50μ.

This grain is fairly abundant but less than *D. densus*, from which it differs in being more oval and with a much smoother surface. These two species are quite like those figured by Raistrick and Simpson (1933) as A 1 from the Plessey, Tilley, and Beaumont coals of Northumberland, England. I would refer those forms to this genus.

Slide L1 (85.4x47.1).

Denso-sporites densus sp. nov.

Fig. 7

Spore more or less spherical or round, wall "b" very thick, very dark and opaque, with a somewhat irregular surface; central portion "a" more or

less clear and somewhat triangular in shape; in most cases apparently connected with the outside by a fine split leaving one corner of the central portion. Diameter about 50μ.

This form is fairly common and easily distinguished from the preceding species, where I have commented upon similar forms.

Slide L1 (77.2x47.8).

Denso-sporites (?) quadratus sp. nov.

Fig. 10

Outline more or less circular apparently with double wings "c" on either side; wall "b" thick, opaque, about one-third the diameter; on the side away from the wings there are usually (may be more or less) five gaping silts or cracks "d," or areas of nearly clear material; central portion "a" more or less clear, connected with the outside by a faint line to the middle area of the winged side. Width at wings about 85μ; diameter of opaque part about 42μ.

On this spore, which is very rare, there are what I take to be wings (Fig. 10c). These projections, where they overlap, are as opaque as the wall "b" but at the ends where they are not overlapping they are quite thin. The clear places "d" may be cracks in the wall due to drying, or some other cause but in all cases the clear placed "d" are surrounded by the thin line which surrounds the entire grain.

Slide L1 (87.6x46.8).

Genus **Elongato-sporites** gen. nov.

Characterized by the elongate shape of the spore, and what appears to be irregularly spaced lengthwise wings. Genotype: *Elongato-sporites reticulatus.*

Elongato-sporites reticulatus sp. nov.

Fig. 12

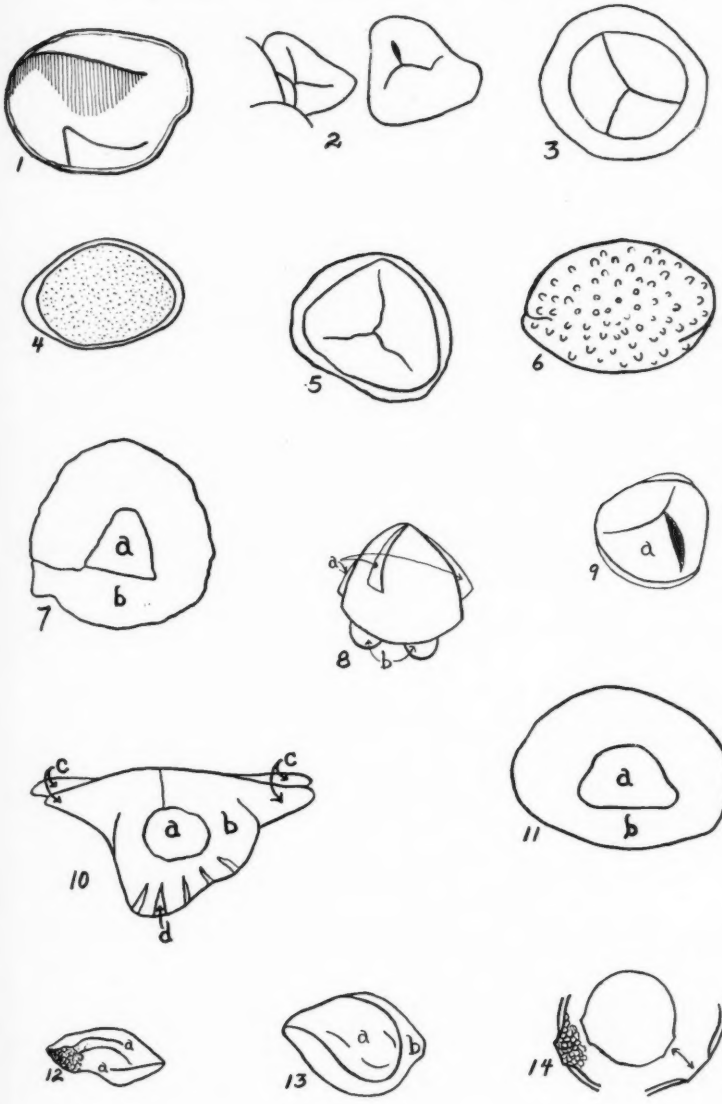
Spore elongate ovate; acute; wall thin, finely reticulate, ornamented by ridges or wings beginning at the points and running a little over half the

EXPLANATION OF PLATE

FIGURES

1. Laevigato-sporites cranmorensis W. Berry.
2. Zonales-sporites Priddyi W. Berry.
3. Zonales-sporites penningtonensis W. Berry.
4. Laevigato-sporites pennovalis W. Berry.
5. Zonales-sporites peacocki W. Berry.
6. Tuberculati-sporites tuberculatus W. Berry.
7. Denso-sporites densus W. Berry.
8. Sporonites tripterus W. Berry.
9. Zonales-sporites irregularis W. Berry.
10. Denso-sporites (?) quadralis W. Berry.
11. Denso-sporites covensis W. Berry.
12. Elongato-sporites reticulatis W. Berry.
13. Laevigato-sporites rheaensis W. Berry
14. Sporonites biporus W. Berry

All figures enlarged 497.3 times.


1
2
3
4
5
6
a
b
7
a
b
8
a
9
c
c
a
b
10
d
a
b
11
12
a
a
13
a
b
14

length of the spore, irregularly placed; margins more or less keel-like making it appear that the spore is triangular in cross-section; color usually brown. Length 35μ, width 15μ.

This elongate spore is among the most common forms in this coal. Its elongate shape and ridged surface make it easily recognizable. It is somewhat like the spore figured by McCabe (1931, pl. 3, fig. 5) from the No. 5 coal of Fulton County, Illinois. McCabe's form can be referred to this genus.

Slide L1 (93.2x49.8).

Genus *Sporonites* H. Potonié 1893

Sporonites biporus sp. nov.

Fig. 14

Spore spherical; wall very thin, double except at two places where the double wall is replaced by what are apparently flat diaphragms; these diaphragms are not curved as is the rest of the wall and are very thin; surface reticulate except at the diaphragms. Diameter about 20μ.

Slide L1 (82.3x52).

Sporonites tripterus sp. nov.

Fig. 8

Spore somewhat like a round-based cone, with three narrow wings "a" radially arranged, beginning at the apex and extending about two-thirds of the way down the sides; the "base" of the spore bearing two hemispherical bumps each about one-fourth the width of the base. There may be a third one, but in the several specimens observed only two were ever visible; if three are present they alternate with the wings. If, as it appears, there are but two, they are not necessarily in any fixed position relative to the wings. Height of the entire spore 39μ.

This form is very rare.

Slide L1 (78.5x45).

REFERENCES

REINSCH, P. F. 1884—Micro-Palaeo-Phytologia Formationes Carboniferae **1** (London).

BENNIE, I. AND R. KIDSTON. 1888—On the occurrence of Spores in the Carboniferous Formation of Scotland. Proc. Royal Phys. Soc. Edinburgh **9**:82-117.

MCCABE, LOUIS C. 1931—Some Plant Structures of Coal. Trans. Ill. Acad. Sci. **24**(2):321-326.

POTONIE, R., IBRAHIM, A. AND R. LOOSE. 1932—Sporenformen aus den Flözen Aegir und Bismarck des Ruhrgebietes. N. Jahrb. f. Min. etc. Beil. Bd. **67**(B): 438-454.

IBRAHIM, A. C. 1933—Sporenformen des Aegirhorizonts des Ruhr-Reviers. Dissertation, Technische Hochschule, Berlin 1932 (1933).

RAISTRICK, A. AND J. SIMPSON. 1933—The Microspores of some Northumberland Coals, and their use in the correlation of Coal-Seams. Trans. Inst. Min. Engin. **85**(4):225-235.

DUKE UNIVERSITY,
DURHAM, N. C.
DEPT. OF GEOLOGY,

making
brown.

oal. Its
omewhat
. 5 coal
genus.

here the
nese dia-
; surface

ings "a"
ls of the
l bumps
e, but in
present
are not
he entire

London).
oniferous

ead. Sci.

zen Aegir
67(B):

Disserta-

mberland
n. Engin.